DIET, HABITAT, AND ECOMORPHOLOGY OF CICHLIDS IN THE UPPER BLADEN RIVER, BELIZE

A Thesis

by

JENNIFER L. COCHRAN

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

August 2008

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

Chair of Committee,	Kirk O. Winemiller
Committee Members,	Steven Davis
	Gil Rosenthal
Head of Department,	Thomas Lacher, Jr.

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ABSTRACT

Diet, Habitat and Ecomorphology of Cichlids in the Upper Bladen River, Belize.

(August 2008)

Jennifer L. Cochran, B.S.; M.A., Saint Mary's University of Minnesota

Chair of Advisory Committee: Dr. Kirk O. Winemiller

Cichlids are among the most species rich and ecologically diverse families of freshwater fishes. Life history attributes vary greatly among cichlids across their global range, and in the Neotropics alone studies have revealed a great deal of diversity in cichlid ecology, morphology and behavior. This study investigated the habitat use, diet, and ecomorphology of an assemblage of cichlids in the Upper Bladen River, Belize. Mesohabitats, including riffles, runs, deep pools, vegetated areas and adjacent streams, were surveyed and snorkeled, and physicochemical and habitat variables were measured at each site where cichlids were observed or collected. Between 12 and 65 stomachs of each cichlid species were analyzed for diet composition. In addition, traditional morphometrics were completed on five individuals of each species in order to investigate the relationships between morphology, diet, and habitat use. The present study revealed patterns of trophic and morphological diversity consistent with a hypothesis of resource partitioning in accordance with adaptive divergence in morphological traits that influence ecological performance. The Bladen cichlid assemblage has one algivore with a long, coiled gut (*Archocentrus spilurus*), one piscivore with an elongated body and highly protrusbile jaws (*Petenia splendida*), two substrate sifters that feed extensively on benthic invertebrates (*Astatheros robertsoni* and *Thorichthys meeki*), one midwater invertebrate feeder

(‘*Cichlasoma’ salvini*), and one large-bodied, trophic generalist (*Vieja maculicauda*). Species in this assemblage display divergent ecological patterns supported by morphological and behavioral adaptations that yield a degree of diet and habitat segregation. The present study provides not only basic ecological data essential for effective conservation, but also evidence of niche diversification within a local assemblage of heroine cichlids that will be useful for ecological and evolutionary analyses at larger scales of taxonomy, geography, and time.

DEDICATION

To my father

who let me tag along

To my mother

for reminding me to walk by faith and not by sight

To Trevor

for your patience, support and love. I will always love you more than yesterday.

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I would like to thank foremost, my advisor and committee chair, Dr. Kirk Winemiller, for his academic support and mentorship from the beginning until the end. My field work was funded by a grant from the National Science Foundation.

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INTRODUCTION*

Background

Cichlids are among the most species-rich and diverse families of freshwater fishes, with a range in the Eastern Hemisphere extending throughout Africa and parts of the Middle East, including Madagascar, Sri Lanka, and along the southern coast of India. In the Western Hemisphere, cichlids occur from southern Texas to Argentina. Within the Perciformes, cichlids are placed in the suborder Labroidei, a large assemblage containing over 1800 species, or 5-10% of all living fishes. Members of this suborder possess highly derived pharyngeal jaws, a configuration referred to as the "labroid pharyngeal jaw". Recent research suggests that the labroid pharyngeal jaw had important evolutionary consequences that have prompted significant diversification within the group, as it has allowed for development of diverse trophic behavior (for examples see: Greenwood 1978, Liem 1986, Gobalet 1989, Liem 1991).

Life history and other ecological attributes vary greatly among cichlids across their global range. In the Neotropics alone, studies have revealed a great diversity in cichlid ecology, morphology and behavior (Lowe-McConnell 1991, Winemiller et al. 1995). This great diversity, in addition to providing evidence of rapid evolution, is the reason why cichlids provide a valuable resource for studies of speciation and adaptive radiation (Meyer 1987, Farias et al. 1999).

Adaptive radiation is morphological and ecological diversification within a lineage undergoing rapid phylogenesis, and the phenomenon has been studied extensively based on cichlid species flocks in the Great Lakes of Africa. Adaptive radiation occurs when an ancestral lineage evolves into multiple species with different traits that allow

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*This thesis follows the style and format of Ecology.

them to inhabit a variety of different environments or niches (Schluter 2002). Trophic differentiation presumably caused or accompanied radiation into various ecological niches (Liem 1991). Cichlids of the Neotropics have undergone impressive speciation as well, however, in a different pattern and representing a much older diversification than those of African lakes (Kullander 2003, Lopez-Fernandez et al. 2005). Among the extensive trophic diversification undergone by Neotropical cichlids (Myers 1966, Stiassny 1991, Winemiller et al. 1995), the Heroines are considered to be the most trophically diverse cichlid group (Hulsey et al. 2004) and specialize on a wide variety of distinct prey groups ranging from insects, algae, and detritus to evasive prey such as fish and crustaceans (Eaton 1943, Valtierra-Vega and Schmitter-Soto 2003, Waltzek and Wainright 2003).

Ecomorphology plays a central role in the study of adaptive radiation. Ecomorphology is an approach that examines ecological characteristics or performance functions of morphological features. The ecomorphological paradigm infers that morphological features are adaptive, i.e. they evolve and diversify due to competition, predation or other biotic interactions (Bock 1990). Using morphological traits to predict species or community patterns of food and habitat use is one avenue of ecomorphological studies (Wainwright and Richard 1995).

Studies of fish ecomorphology are particularly informative, because fishes exhibit extensive morphological and ecological diversity and relationships between form and function have been well established for many easily measured traits (Motta et al. 1995). Evolutionary ecology and ecomorphology have been investigated extensively for the family Cichlidae (Lowe-McConnell 1969, Lowe-McConnell 1991, Kullander et al. 1992,

Norton and Brainerd 1993, Winemiller et al. 1995, Jepsen et al. 1997, Kornfield and Smith 2000, Ruber and Adams 2001). It has been suggested that Central American cichlid assemblages show greater ecomorphological diversification than African cichlid assemblages in rivers containing comparable numbers of species. One possible reason for adaptive radiation among Central American cichlids may be an evolutionary history lacking competition and predation from other freshwater fish families containing large numbers of taxa, as found in Africa and South America (Winemiller 1991, Winemiller et al. 1995).

Objectives

A primary goal of ecology is to obtain resource use data that may be useful for explaining how habitats maintain large numbers of species (Hutchinson 1959, Rosenzweig 1995, Roy et al. 2000). Given that global threats to biodiversity have become a critical issue in conservation biology, it also has become increasingly important to recognize and investigate how biodiversity influences the function of ecosystems (Loreau et al. 2001). Although there have been many empirical and theoretical advances in community ecology, details of species' coexistence and interactions are still being investigated (Chesson 2000, Hubbell 2001, Leibold et al. 2004). An early explanation for the maintenance of local species diversity is species packing, fine-scale niche partitioning by resource specialists (Dobzhansky 1950). In habitats supporting large numbers of closely related species, one would expect to find evidence of species being morphologically adapted, or specialized, to specific niches. In addition to exhibiting extremely specialized morphologies (Eaton 1943, Barel 1983, Hoogerhoud 1986, Hulsey

and García de León 2005), cichlids also provide evidence of niche partitioning (Winemiller et al. 1995). Cichlids, in general, are considered one of the most ecologically and functionally diverse families of freshwater fishes (Barlow 2000).

Classic studies of African Rift Lake cichlids questioned why so many of the obvious specialists with extreme morphologies were also generalists for much of the year (Liem 1980, 1991). Liem proposed that specializations provide access to food during annual periods of intense competition. Since then, others have argued that such specialization is shaped by optimal foraging in addition to an uneven relationship between favored prey items and their availability. Most of the time, fish should eat preferred prey, regardless of whether they are morphologically specialized and capable of consuming other taxa in a competitively superior way (Robinson and Wilson 1998). The present study does not seek to prove or disprove either of these theories, but instead examines the extent to which morphological and niche specializations are linked, and evaluates the possible contribution of morphologically-based niche partitioning in the coexistence of a species assemblage of Heroine cichlids in the Upper Bladen River, Belize. This was done through investigations of diet, habitat use and ecomorphology, and included the following cichlids: *Archocentrus spilurus*, *Astatheros robertsoni*, *'Cichasoma' salvini*, *Thorichthys meeki*, *Vieja maculicauda* and *Petenia splendida*.

This study investigates ecological aspects of a local cichlid assemblage that is one of many Neotropical cichlid assemblages that will ultimately be examined in a broader investigation of the diversification of Neotropical cichlids. The null hypothesis is that there is no evidence of habitat and diet partitioning associated with divergent species morphologies. Alternatively, there may be significant differences in habitat use and diet

based on morphological variation. If functionally based trophic and habitat specialization is the key to biodiversity in cichlid communities, we would expect to see a close relationship between functionally significant morphological attributes and patterns of diet and habitat use. Alternatively, if niche partitioning is relatively unimportant, we would predict that multivariate analysis would illustrate weak patterns of relationship between trophic structures and body form with diet and habitat.

In addition to investigating relationships between morphology and ecological performance, this study also aimed to provide a descriptive overview of diet and habitat use of the cichlids within this assemblage. To date there are very few systematic, quantitative studies of diet and habitat use of Mesoamerican cichlids (for examples see Martinez-Palacios and Ross 1987, Winemiller et al. 1995, Valtierra-Vega and Schmitter-Soto 2000). Whereas Belize currently provides significant environmental conservation, many areas of Central America have few enforced regulations or laws concerning agriculture, economic development, and recreational and artisanal fisheries. In order to develop and implement management and conservation strategies, quantitative investigations such as the present study will be critical.

With this in mind, the specific objectives of this study were: 1) to investigate diet composition and habitat use of cichlids present in the Upper Bladen River; 2) to characterize these differences using multivariate statistical methods; 3) to use multivariate statistical methods to explore how habitat use and diet composition may be constrained by morphological features; and 4) to investigate correlations among diet, habitat, and morphological indices. I expected each cichlid species to occupy a distinct morphospace and that some of their differing morphological attributes would be

significantly correlated with habitat use and diet. Additionally, I hypothesized that these analyses would reveal evidence of niche partitioning within this cichlid assemblage.

METHODS

Study area

This study took place within the southeast portion of the Bladen Nature Reserve, in the Toledo District of southern Belize in December 2006 and January 2007 (16°34'N, 88°43'W, ca 45 m elevation) (Fig. 1). The headwaters of the Bladen River originate within the Bladen Reserve, and are a part of the Monkey River Basin. This system lies along the southeastern flank of the Maya Mountains and contains three branches (including the Trio and the Swasey) making it the fourth largest river basin in Belize (1275 km^2) (Esselman et al. 2006). From the headwaters through the sampling area, the Bladen River lies within contiguous government protected nature reserves and flows through the Maya Mountains, which are heavily blanketed with largely undisturbed broadleaf rainforest. Figure 2 provides a more detailed illustration of the sampling area.

The climate in southern Belize is considered tropical with an average temperature of 21°C. The vegetation is dominated by undisturbed tropical broadleaf rainforest, and annual rainfall is approximately 2500–3000 mm in distinct wet and dry seasons, causing periods of flooding and drought. Precipitation is highest from July to October, a period that accounts for approximately 84% of the total annual discharge (Heyman and Kjerfve 1999).

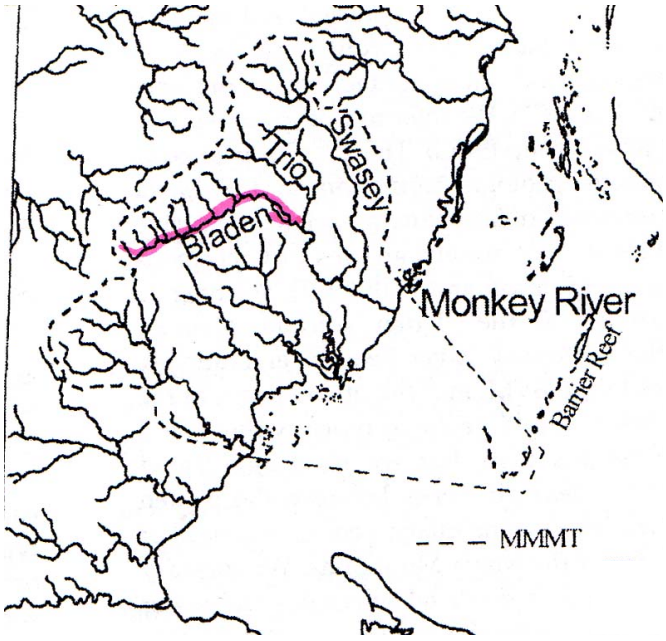


FIG. 1. Map of southern Belize illustrating the major branches of the Monkey River, including the Bladen River.

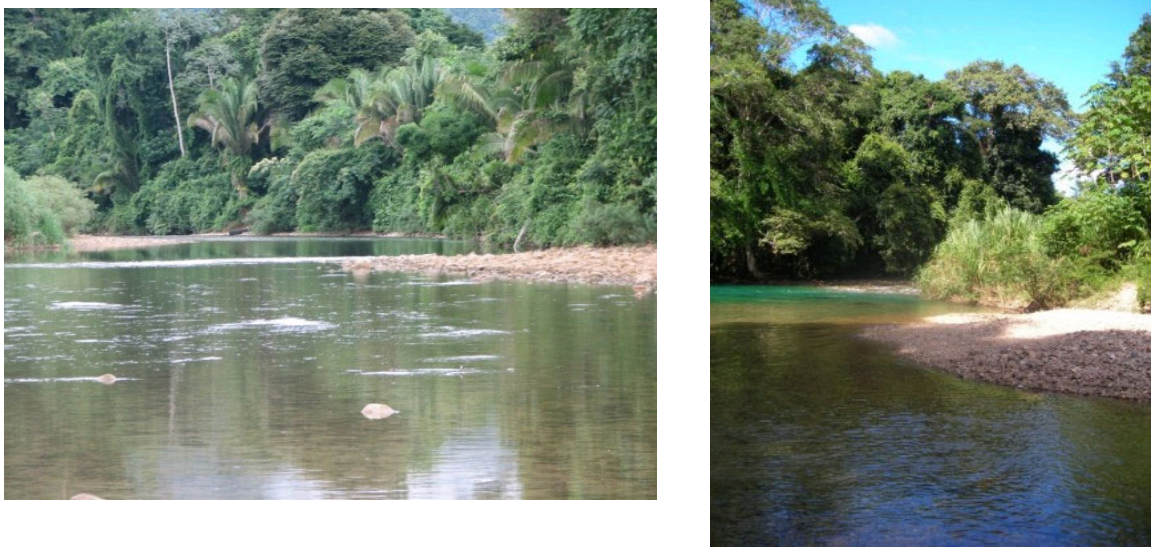


Fig. 2. Examples of habitats in the upper Bladen River where sampling took place. The river is lined with undisturbed primary forest and the substrate is largely comprised of a mixture of cobble, rocks, and sand (photos by Jennifer Cochran).

Habitat

Sampling took place in a variety of mesohabitats including riffles, runs, deep pools, vegetated areas and adjacent streams. Several physicochemical variables were investigated at each site where fish were observed or collected. Temperature (°C), dissolved oxygen concentration (mg/L), salinity (ppt), and conductivity (µs) were measured using a YSI model 85 meter, and pH was determined with a handheld electronic pH meter. Maximum water depth and channel width were measured using a weighted measuring tape, and transparency was determined with a Secchi disk. Flow velocity (m/s) was measured by timing the amount of time in took for a neutrally buoyant object to travel across a known distance.

In addition to physiochemical variables, other habitat characteristics were recorded at each site where fish were collected, including presence of aquatic vegetation, structural density, substrate composition, and types of structure present. Substrate categories were defined as bedrock, silt, sand, mud, leaf litter, woody debris, gravel (< 3 cm diameter), cobble (4-10 cm diameter), rock (11-25 cm diameter), and bedrock(> 26 cm diameter).

Habitat data were collected at each site where fish were collected, however, these data were also collected along ten randomly selected transects along a 0.7 km stretch of the main channel where the majority of sampling took place. Transect locations were selecting using random numbers generated from a random number table. Each transect extended across the main channel perpendicular to the shoreline and was clearly marked on shore using a bright yellow piece of cloth. Temperature, pH, dissolved oxygen concentration, conductivity, channel width and bank vegetation were measured once at

each transect. Water depth, flow, substrate types and densities, structural types and densities, and presence of aquatic vegetation were collected at a point every 5.0 m along the transect using a 1.0 m x 1.0 m quadrant. A measuring tape was used to determine the location of each point along the transect line.

After the collection of habitat data along each transect, snorkeling observations were made at the same designated points where habitat data were collected. All species were identifiable from external morphology. Training and testing of accuracy in species identification was provided for each observer prior to observations. Measurements to determine the location of each point were done using a tape measure 10 m downstream of the transect in order to prevent disturbance of fish upstream. The observer then snorkeled upstream, parallel to the shoreline through the transect line observing all fish that were approximately one meter on either side of the line. Snorkeling at each point was done for approximately 5 minutes. The observer visually identified and counted individuals of all fish species and one person on shore recorded data and time. After each point was snorkeled, five minutes was allowed to pass before snorkeling the next point in order to minimize the effect of fish disturbance. In addition, during both habitat sampling and snorkeling surveys, all movement between transects was done on shore to prevent disturbance as well.

Once all habitat and snorkel data were compiled, a vegetation index, substrate index, and structural index were calculated for each transect point and collection site. Each index was calculated by dividing the total number of categories observed at the location or point by the maximum observed categories. The indices were used to

calculate an overall index of habitat complexity. The following equation was used to calculate the index of habitat complexity:

$$\frac{\text{Vegetation index + Substrate Index + Structural Index}}{3}$$

The habitat index was calculated for each individual fish that was either observed and collected, and then an average was found for each species. These values were then correlated to each species' dietary breadth using the Pearson product-moment correlation coefficient, *r*.

Species pair-wise similarities were estimated using Jaccard's Index. This index was calculated based on sites (transect points) occupied by cichlids to determine which species exhibited the greatest pair-wise associations. Co-occurrence across all points in each transect was determined, and then the index was calculated among all species pairs as follows:

$$=A/(A+B+C),$$

where A = number of sites occupied by both species (i.e. *A. spilurus* and *C. salvini*), B = number of sites occupied by one species (*A. spilurus*), but not the other fish species (*C. salvini*) , and C = number of sites not occupied by one species (*A. spilurus*), but occupied by the other species (*C. salvini*). Scores ranged from 0 to 1, and the greatest scores indicate those cichlid pairs with the strongest associations.

Diet

Between 30 and 50 adult specimens, when available, of each species were euthanized and placed in 10% formalin (Table 1). Individuals were later stored in 70%

ethanol and dissected for dietary analysis using methods similar to those described by Winemiller (1990) involving microscopic examination and volumetric estimation of gut contents. Food items in the anterior portion of the gut were removed and examined under a dissecting microscope and identified according to appropriate prey categories listed in Appendix I. Invertebrates were classified to the lowest feasible taxonomic level according to keys and descriptions in Pennak (1978). Prey items were sorted, blotted dry, and measured in a graduated cylinder by water displacement. Volumes of items ≥ 0.25 ml were measured using this method, and those smaller than 0.25 ml were estimated using a piece of graph paper with 1.0 x 1.0-mm squares (1.0 mm^3 was equivalent to 0.001 ml of diet item). The paper was placed beneath the Petri dish containing the diet items under investigation, and then diet volume was estimated using either a binocular dissection microscope or a compound light microscope when necessary. In the case of *A. spilurus*, whose diet was composed of mostly algae and detritus, diet was estimated by removing and weighing the anterior one-third of the gut. The upper intestinal tract was then opened, and a small portion of its contents was removed and placed on a slide and covered with a cover slip. The sample was then placed under a compound light microscope, and contents were sorted and grouped according diet item. The total percentage on the slide of each diet item was estimated and converted into milliliters by multiplying the percent value by the total volume of the stomach. Upon completion, the diet composition of each species was quantified using frequency of occurrence and relative total volume of each diet item.

Table 1. Sample sizes and minimum, maximum and mean length of specimens used to investigate the diets of cichlids in the Bladen River (n= number of stomachs examined with food items; ES= number of empty stomachs).

Species	n	ES	Standard length (mm)		
			Min	Man	Mean
A. robertsoni	3	0	88.7	103.5	97.4
P. splendida	12	8	47.2	337.0	203.9
V. maculicauda	23	4	87.5	225.0	147.7
T. meeki	52	4	43.1	90.3	67.0
C. salvini	56	13	47.4	94.2	73.3
A. spilurus	65	1	42.4	72.2	54.9

Diet overlap was estimated with Pianka's (1974) symmetrical niche overlap:

$$\phi_{jk} = \frac{\sum p_{ij} p_{ik}}{\sqrt{(\sum p_{ij}^2 \sum p_{ik}^2)}}$$

where p_{ij} and p_{ik} represent the volumetric proportion of the prey category *i* in the diet of consumer species *j* and *k*. Values for the symmetrical overlap index range from 0 which indicates no overlap to 1 indicating a complete overlap, or identical diets for consumer species *j* and *k*. Diet overlap was also correlated with Jaccard's index of co-occurrence using Spearman's Rank correlation in order to assess pair wise similarities in trophic and habitat use.

Niche breadth (B_j) for each consumer species *j* was calculated using Levin's (1968) measure:

$$B_j = \frac{1}{\sum p_{ij}^2}$$

where p_{ij} is the volumetric fraction of prey item *i* in the total diet of consumer species j (Levins 1968). Values of B_j range from 1, indicating a minimum niche breadth or maximum specialization, to *n*, where *n* is equal to the total number or resource states (or prey categories) indicating a maximum niche breadth and minimum specialization (Krebs 1999). In this study there were a total of 23 prey categories (Appendix 1). Niche breadth was standardized in order to make comparisons between species using Hurlbert's (1978) method (Krebs 1999):

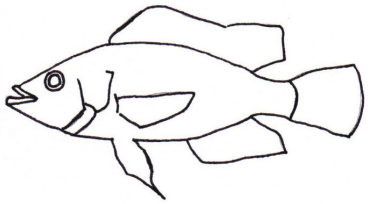
$$B_A = \frac{B_j - 1}{n - 1}$$

where B_A is Levin's standardized niche breadth for consumer species j, with values ranging from 0 to 1, indicating minimum and maximum niche breadth, respectively (Krebs 1999).

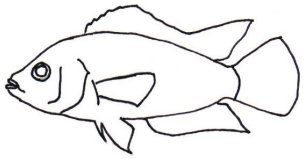
Morphology

Body forms of the six cichlid species that occur in the upper Bladen River are varied (Fig. 3 a-f). Traditional morphometrics were measured on between three and five preserved adult specimens of each cichlid species, depending on availability (Table 2). Measurements above 130 mm were taken to the nearest 1.0 mm using a measuring tape, and those ranging between 0.5 mm were taken to the nearest 0.1 mm using calipers. Structures smaller than 0.5 were measured using an ocular micrometer attached to a dissecting microscope. All measurements were taken as the straight-line distance between points.

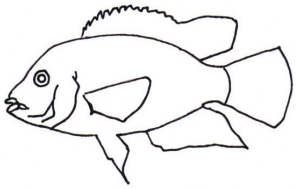
A) *Petenia splendida*



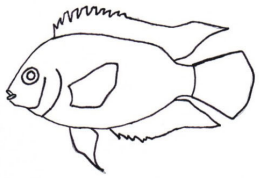
B) 'Cichlasoma' salvini



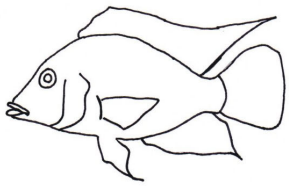
C) *Vieja maculicauda*



D) *Archocentrus spilurus*



E) *Astatheros robertsoni*



F) *Thorichthys meeki*

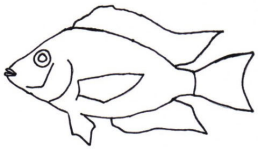


FIG. 3A-F. Body forms of cichlids found in the upper Bladen River. Illustrations were adapted from Greenfield and Thomerson (1997).

TABLE 2. Minimum, maximum and mean sizes of individuals of each species used to investigate morphology.

		Standard Length (mm)		
Species	n	Min	Max	Mean
A. spilurus	5	68.3	73.9	71.3
C. salvini	5	55.9	96.9	81.8
T. meeki	5	54.8	90.3	75.7
A. robertsoni	3	88.7	103.5	97.4
V. maculicauda	5	116.8	162.8	149.2
P. splendida	5	199	337.0	252.2

Morphological characters were chosen that related to feeding, swimming behavior, and habitat (Gatz 1979). The following characters were measured as follows:

1) maximum standard length (MSL)—largest standard length for specimens collected at a site;
2) maximum body depth (BODD)—maximum vertical distance from dorsum to ventrum;
3) maximum body width (BODW)—maximum horizontal distance from side to side;
4) caudal peduncle depth (PEDD)—minimum vertical distance from dorsum to ventrum of the caudal peduncle;
5) caudal peduncle width (PEDW)—width of the caudal peduncle in horizontal plane at midlength;
6) body depth below midline (BDBM)—vertical distance from midline to ventrum, midline defined as the imaginary line passing from the pupil of the eye through the center of the ultimate vertebrae;
7) head length (HEAL)—distance from tip of upper jaw to the most caudal extension of the operculum;
8) head height (HEAH)—vertical distance from dorsum to ventrum passing through the pupil;
9) interorbital distance (INORB)—maximum horizontal distance between both orbits;
10) eye position (EYEP)—vertical distance from the center of the pupil to ventrum;
11) eye diameter (EYED)—horizontal distance from eye margin to eye margin;

12) mouth position (MOUPO)—estimated by drawing a reference horizontal line that passes from the corner of the mouth to the middle of the insertion of caudal rays in the caudal peduncle. With the fish fixed in this position, a point was found equivalent to the anterior-most point of the orbit, and another corresponding to the tip of the upper lip. A line was traced between the two points and the angle between the two was measured with a protractor;
13) gape width (GAPE)—horizontal distance inside fully open mouth at widest point;
14) snout length closed (SNTC)—distance from the anterior edge of the orbit to the center of the upper lip;
15) snout length open (SNTO)—distance from the anterior edge of the orbit to the center of the upper lip with mouth fully protruded;
16) dorsal fin height (DORH)—maximum distance from proximal to distal margin of the dorsal fin (excluding filaments);
17) dorsal fin length (DORL)—distance from anterior proximal margin to posterior proximal margin of the dorsal fin;
18) pectoral fin length (PECTL)—maximum distance from proximal to distal margin of the pectoral fin;
19) pectoral fin height (PECTH)—maximum vertical distance across the fully spread pectoral fin;
20) caudal fin length (CAUDL)—maximum distance from proximal to distal margin of the caudal fin (excluding filament);
21) caudal fin depth (CAUDD)—maximum vertical distance across the fully spread caudal fin;

22) pelvic fin length (PELVL)—the distance from the base of the pelvic fin to the tip of the longest ray (excluding filaments);
23) anal fin length (ANALL)—distance from anterior proximal margin to posterior proximal margin of the anal fin;
24) anal fin height (ANALH)—maximum distance from the proximal to distal margin of the anal fin;
25) gut length (GUTL)—measured from the beginning of the esophagus to the anus (fully extending without stretching);
26) ceratobranchial length (CERL)—taken on dissected first ceratobranchial. The straight distance between the joint of the basibranchial with the ceratobranchial and the joint between the ceratobranchial and the epibranchial;
27) ceratobranchial gill-raker number (GILRN)—number of rakers between the anterior tip of the ceratobranchial and the corner of the epibranchial;
28) ceratobranchial inter-gill-raker space (INTRS)—the average distance between the ceratobranchial gill-rakers;
29) ceratobranchial gill-raker length (GILRL)—the average distance between the base of the gill-rakers and their tip;
30) lower pharyngeal jaw width (LPJW)—maximum distance between the horns;
31) lower pharyngeal jaw length (LPJL)—maximum distance from the imaginary midline between the caudal edge of the horns and the anteriormost tip of the plate;
32) lower pharyngeal jaw depth (LPJD)—maximum distance between the dorsal surface of the plate and the ventral keel joining both toothplate bones;

Multivariate analysis

For each species, measurements and counts of morphological variables for each species were averaged, log transformed and regressed against the log of standard length. In this manner, the morphological variables are descriptors of body and fin shape, without the influence of body size. Allometric influences are negligible in interspecific comparisons in which a single size class is chosen to represent a given species, however, allometry was reduced by log transforming the data (Winemiller 1991). Principal components analysis (PCA) was then used to identify patterns in morphological variation among species. PCA is a method of breaking down or partitioning a resemblance matrix into a set of orthogonal (perpendicular) axes or components. Each PCA axis corresponds to an eigenvalue of the matrix. The eigenvalue is the variance accounted for by the axis. The first few PCA axes represent the largest percentage of total variation that can be explained (Ludwig and Reynolds 1988).

Species scores on the first four orthogonal axes were used to calculate pair wise Euclidean distances for comparison with patterns generated by the standardized morphological variables. A matrix of Euclidean distances between species pairs was calculated according to the formula:

$$D_{jk} = \left[\sum_{i=1}^{n} (x_{ij} - x_{jk})^2 \right]^{1/2},$$

where n is the number of PC axes with eigenvalues greater than 1.0 and x_{ij} and x_{jk} are the character loadings on the same PC axis for species pair j and k. From each matrix of Euclidean distances, I identified nearest neighbor (NND) and the distance to the assemblage centroid (CD) for each species. Average NND is an index of species

dispersion in morphological space, the standard deviation of NND serves as an index of the evenness of species dispersion in morphological space (Findley 1973, Ricklefs et al. 1981) and average CD provides and index of niche diversification, or the relative size of the morphological hypervolume defined by an assemblage.

Relationships between morphology and both diet and habitat were explored using canonical correspondence analysis (CCA) using CANOCO for Windows. CCA is a direct gradient technique in which orthogonal canonical axes are derived based on morphology, and express how well the morphological variables explain the variation in diet and habitat (ter Braak 1986). CCA requires that there are fewer independent variables (dietary and morphological variables in this case) than observations (species in this case), therefore, the number of diet categories was reduced from 23 to 8, using only major functional groups. A resource matrix was built containing the volumetric dietary proportions of each diet item for each fish species, and a secondary matrix included the residuals of the regression of log transformed morphological variables against the log of the standard length. Using residuals eliminates the correlation to size and emphasizes the importance of shape (Atchlety et al. 1976, Harvey and Pagel 1991). Effects of both shape and size were of interest; therefore, the values of the log of standard length were included as a variable (Losos et al. 1998). Variables were manually tested for significance using forward-selection, and only significant variables ($p < 0.05$) were retained in the analysis. The statistical significance of canonical axes was calculated using Monte Carlo permutation tests. The null hypothesis that morphological variables do not explain any of the observed variation in diet was tested with an F-ratio of the eigenvalues of the

canonical axes and the residual sum of squares. The default 199 permutations were run to establish a 95% confidence interval (terBraak and Simlauer 1998).

RESULTS

Species-specific findings

Water physicochemistry showed little variance among the habitats that supported upper Bladen River cichlids (Table 3). Channel width (Fig. 4), flow (Fig.5), presence of algae (Fig. 6), water depth (Fig. 7), substrate (Table 4), and types of structure present (Table 5) showed between-habitat variation, and were included in statistical analyses to characterize habitat preferences. *Vieja maculicauda* and *P. splendida* were most often present within narrow channels less than 25 m in width, and within pools measuring between 1.6 and 2.0 m in maximum depth (Figs. 4, 7). *Archocentrus spilurus*, *C. salvini*, and *T. meeki* were most often found in broad shallow stretches of the river that could be characterized as stream runs or glides (Fig. 7).

At least 75 % of all species (except for *T. meeki*) were observed or collected in the presence of algae. Only approximately 51% of all *T. meeki* observed or collected were associated with habitats containing visible stands of algae. Most algae were present on structure, such as rocks, boulders and logs. *Thorichthys meeki* is a substrate sifter, and thus most individuals were associated with areas of soft substrate, such as sand and silt.

Each species occurred within habitats containing at least four of the eight substrate categories. *Petenia splendida* was associated with leaf litter, gravel, cobble and bedrock; and *V. maculicauda* and *T. meeki* occurred over seven substrates (leaf litter, sand, silt, gravel, rocks, cobble and bedrock). Both *A. spilurus* and *C. salvini* were found in association with all eight substrate types.

Four of the five species were associated with all types of structure (leaf litter, snags, rocks, boulder, and submerged trees). *Petenia splendida* was never found in the

presence of rocks. *Petenia splendida* was found in areas with boulders fifty percent of the time and to a lesser extent were observed in deep pool, slow moving pools over substrates of cobble and gravel (56.25%) and near snags and leaf litter (12.5%) (Tables 3, 4, Fig. 5).

The habitat diversity index describes varying levels of heterogeneity associated with vegetation, substrate, structure, and overall habitat complexity. The habitat diversity index was calculated only with data derived from the snorkel surveys. Index values were calculated for each individual cichlid observed during snorkeling surveys. Mean values for each species and each index are reported in Figure 8. The vegetation index ranged between 0 and 1, and indicates whether or not there was an association with filamentous algae, the only aquatic vegetation observed in the study area. *Cichlasoma salvini* had the highest mean value for vegetation diversity index (0.87), followed by *V. maculicauda* (0.85). *Thorichthys meeki* had the lowest mean vegetation index at 0.51 followed by *P. splendida* (0.79).

TABLE 3. Mean values for physicochemical parameters recorded in the habitats where each cichlid species was sampled in the Upper Bladen River.

Species	Temperature (C)	pH	Conductivity (µs)	Salinity (ppt)	Dissolved Oxygen (mg/L)
A. spilurus	23.9	7.7	228.8	0.1	8.09
C. salvini	23.1	7.7	226.7	0.1	7.94
T. meeki	24.1	7.8	225.0	0.1	7.92
V. maculicauda	24.1	7.6	222.5	0.1	7.67
P. splendida	24.1	7.6	222.3	0.1	7.60

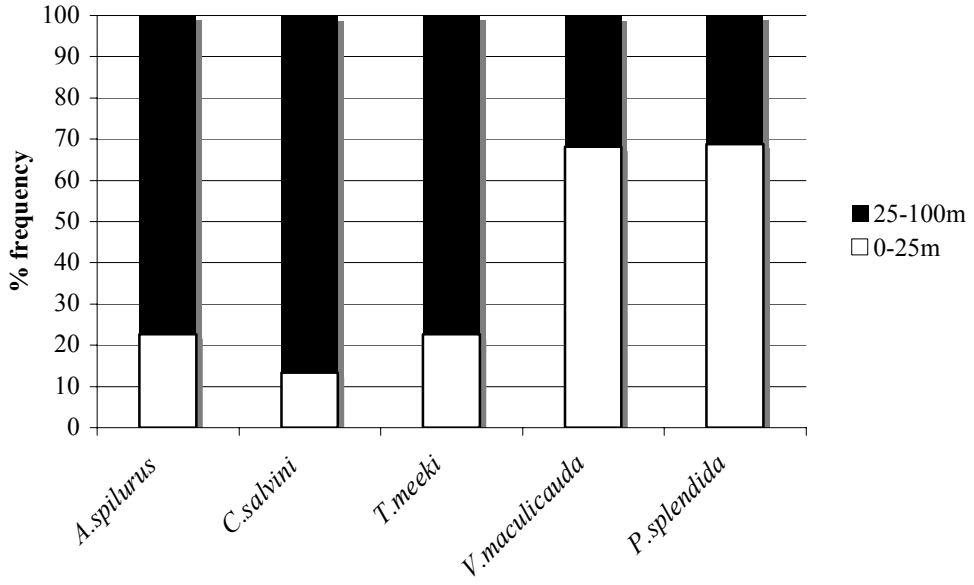


FIG.4. Percent frequency of each species occurring in channel segments less than 25 m in width and those between 25 and 100 m in width.

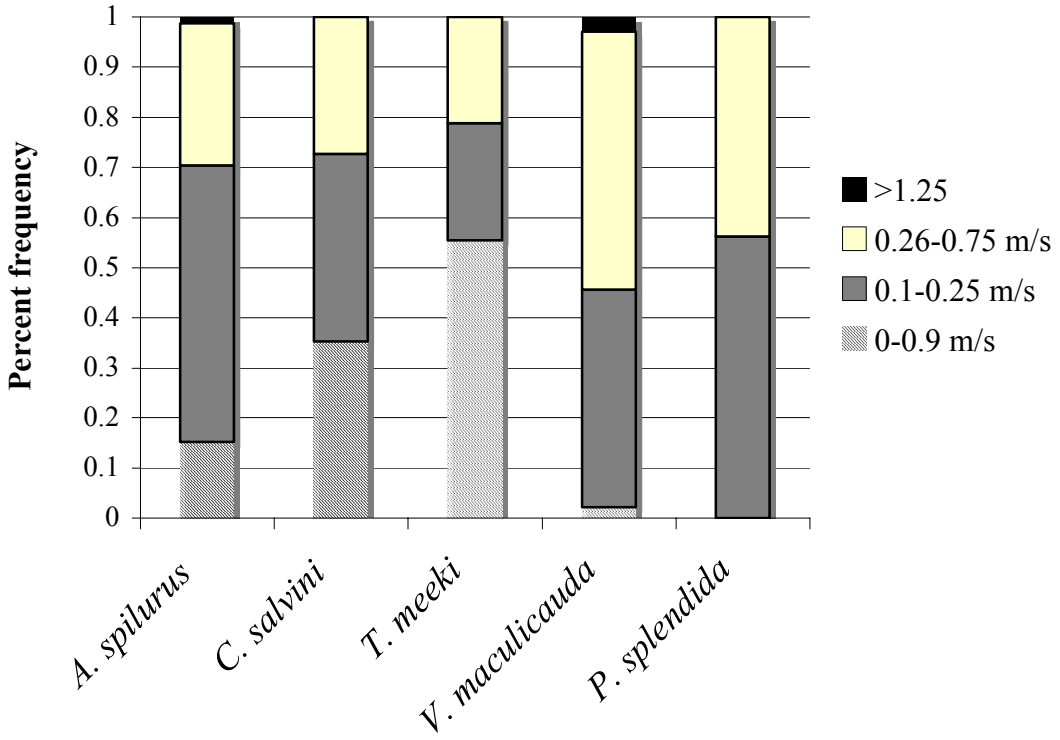


FIG.5. Frequency of occurrence of each cichlid species in habitats with different flow velocities.

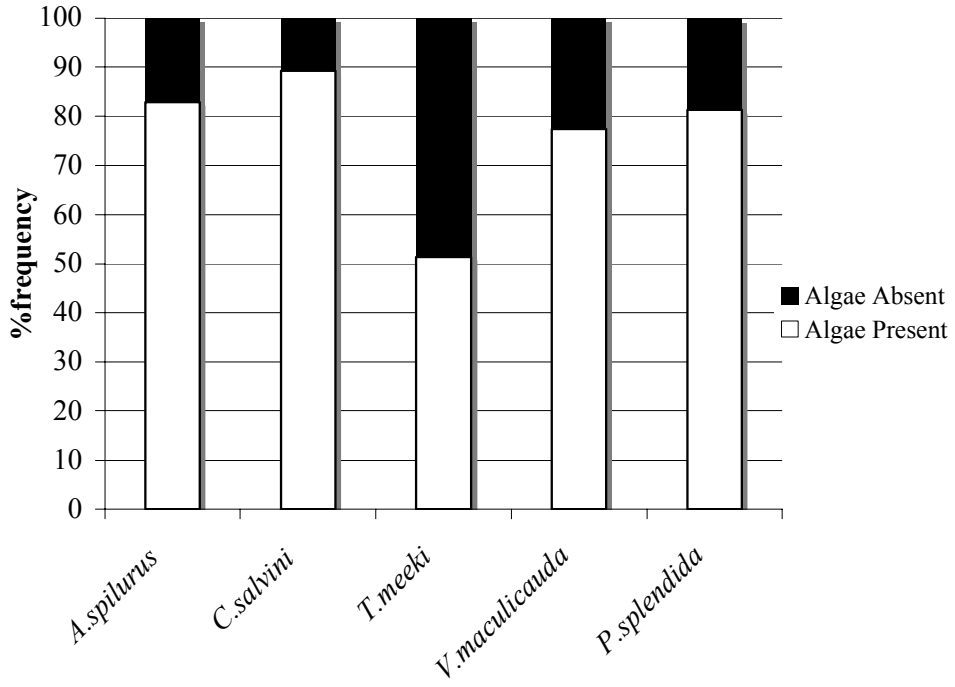


FIG .6. Percentage of individuals of each species observed in habitats with and those without visible stocks of algae.

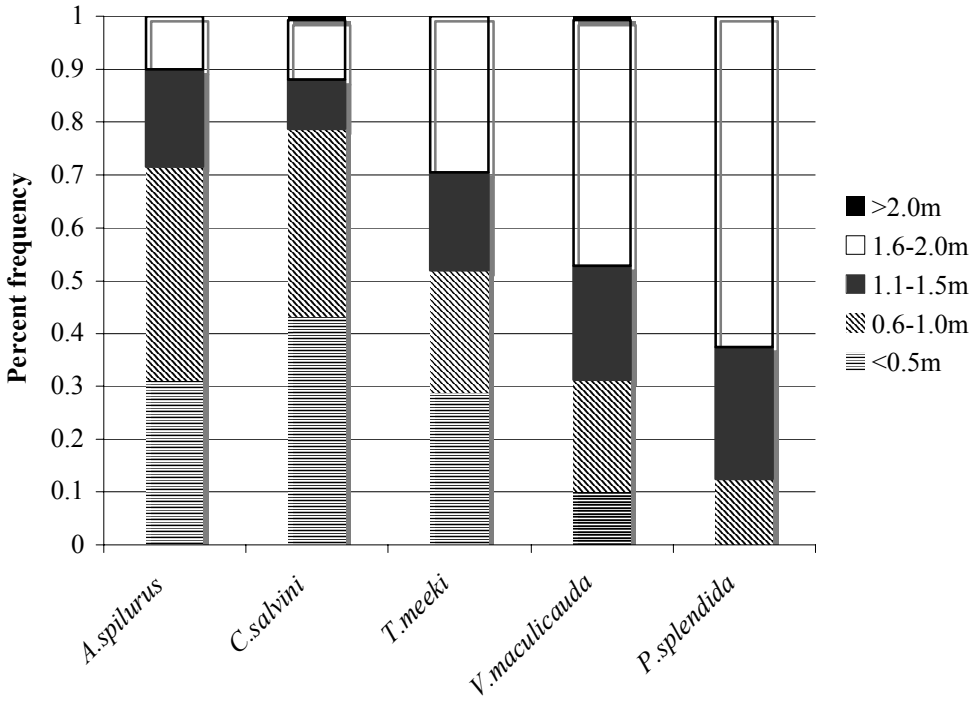


FIG.7. Percent frequency of occurrence of cichlid species in habitats with different water depths.

TABLE 4. Percent frequency of occurrence of cichlid species observed in association with various substrate categories.

	Bedrock	Rocks	Cobble	Gravel	Sand	Mud	Silt	Leaf Litter
A. spilurus	7.25	52.67	80.81	76.97	50.53	7.04	29.68	28.78
C. salvini	11.33	76.67	55.33	58.67	20.0	2.0	38.0	36.67
V. maculicauda	44.93	14.49	47.83	50.72	11.59	0	2.17	9.42
T. meeki	16.20	29.58	46.48	35.21	29.94	12.78	61.97	59.86
P. splendida	50.0	0	56.25	56.25	0	0	0	12.5

TABLE 5. Percent frequency of occurrence of cichlid species in habitats containing various categories of physical structure.

	Submerged trees	Boulder	Rocks	Snag	Leaf litter	None
A. spilurus	8.10	6.40	52.67	18.76	28.78	31.56
C. salvini	30.0	4.67	76.67	26.67	36.67	12.67
V. maculicauda	19.57	23.19	14.49	2.17	9.42	57.24
T. meeki	25.32	7.04	29.58	21.12	59.86	18.31
P. splendida	6.25	50.00	0	12.5	12.5	43.75

A substrate diversity index was calculated for each species based on the eight substrate types observed in the study area: sand, silt, mud, gravel, cobble, rock, bedrock and leaf litter. A high value of structural diversity indicates a more variable or coarse grade of substrate on average. *Petenia splendida* was associated with the highest average value for substrate diversity (0.42) while *V, maculicauda* occurred in areas with the lowest average substrate diversity (0.24).

A structural diversity index was determined for each species based on five types of structure observed in the study area: submerged trees, boulders, rocks, leaf litter and woody snags. *Petenia splendida* had the lowest average values for the structural index (0.09), which reflected the fact that this species was observed most often in the center of large, deep pools approximately 5-10 m from shore, where various physical structures often were uncommon. *Cichlasoma salvini* had the highest average value for the structural index (0.89) and was collected and observed in close association with all types of structures.

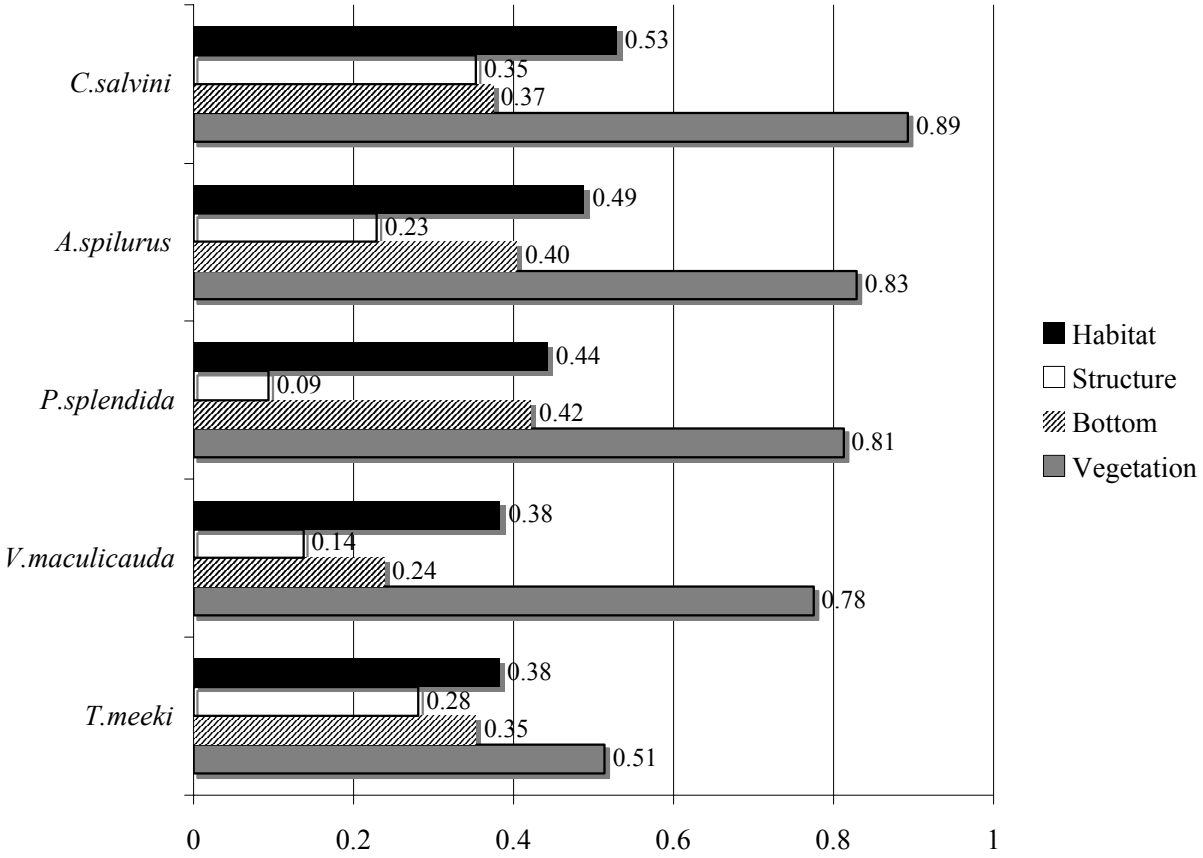


FIG.8. Mean values for indices of overall habitat diversity, structural diversity, substrate diversity, and vegetation diversity.

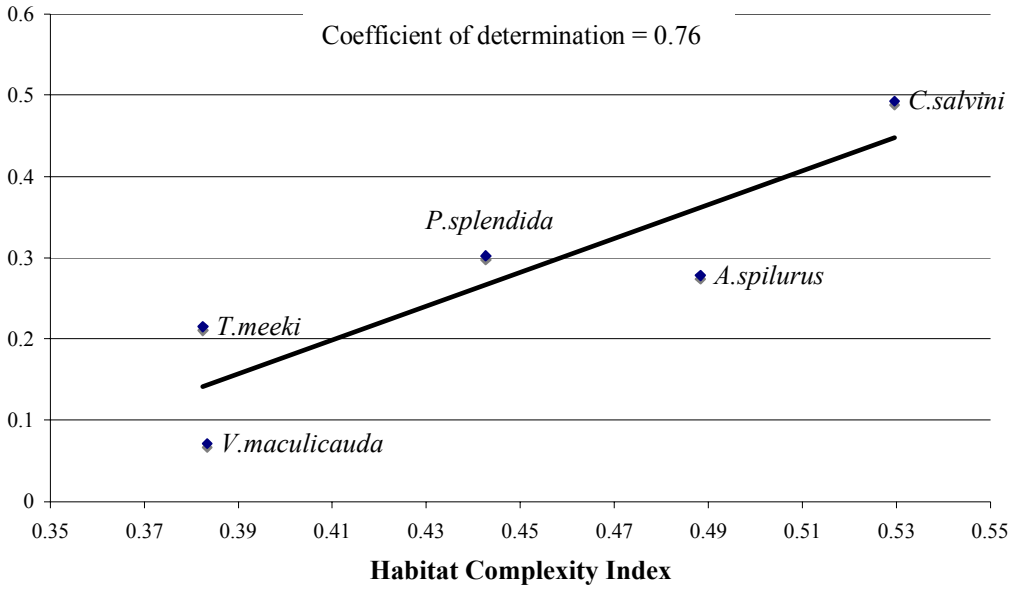


FIG.9. Linear regression of diet breadth and habitat diversity index.

All three indices were used to calculate an overall index of habitat diversity. Species values for habitat diversity vales ranged from 0.38 (*T. meeki* and *V. maculicauda*) to 0.53 (*C. salvini*). Among all species, values for overall habitat diversity were correlated with species diet breadth (Fig.9). Though based on a very small sample size, this relationship had a marginally significant relationship (2-tail, P = 0.053)

Principal components analysis (PCA) was another method used to identify patterns of habitat association among species. The first two PCA axes explained 79 % of accumulated variation (Table 6, Fig. 10). Principal component axis 1 (PC1) explained 43 % of variance, and PC2 accounted for 36.1 % of variance. The first axis was influenced primarily by rocks, bottom index, boulders and depth. Principal components axis 2 was influenced by habitat index, vegetation index, silt and leaf litter. *Archocentrus spilurus* and *C. salvini* were associated with having a high habitat index and vegetation index, whereas *T. meeki* was associated with high amounts of silt and leaf litter, rocks, and a high substrate diversity index. *Petenia splendida* was associated with the presence of boulders and greater depth. *Vieja maculicauda* had high positive loadings corresponding to high values for the habitat diversity index and vegetation index.

TABLE 6. Axis eigenvalues, proportion variation modeled, and variable loadings from principal component analysis with *C. salvini*, *T. meeki*, *A. spilurus*, *V. maculicauda* and *P. splendida* using species averages of habitat variables.

	PCA axis	
	1	2
Eigenvalue	9.175	6.660
Proportion of variation	45.9	33.3
Cumulative variation	45.9	79.2
Channel Width	-0.228	0.277
Depth	0.299	0.048
Flow	0.020	-0.358
Boulder (substrate)	0.316	-0.009
Rock (substrate)	-0.293	-0.076
Cobble (substrate)	-0.091	-0.329
Gravel (substrate)	0.150	-0.274
Sand (substrate)	-0.292	-0.010
Leaves (substrate)	-0.146	0.347
Silt (substrate)	-0.119	0.359
Boulder (structure)	0.317	-0.036
Rock (structure)	-0.299	-0.046
Submerged trees (structure)	0.216	0.116
Snag (structure)	0.220	0.093
Structural density	0.251	-0.074
Algae	-0.178	-0.295
Vegetation Index	-0.003	-0.384
Substrate Index	-0.164	-0.089
Structural Complexity Index	-0.270	-0.062
Habitat Diversity Index	-0.201	-0.280

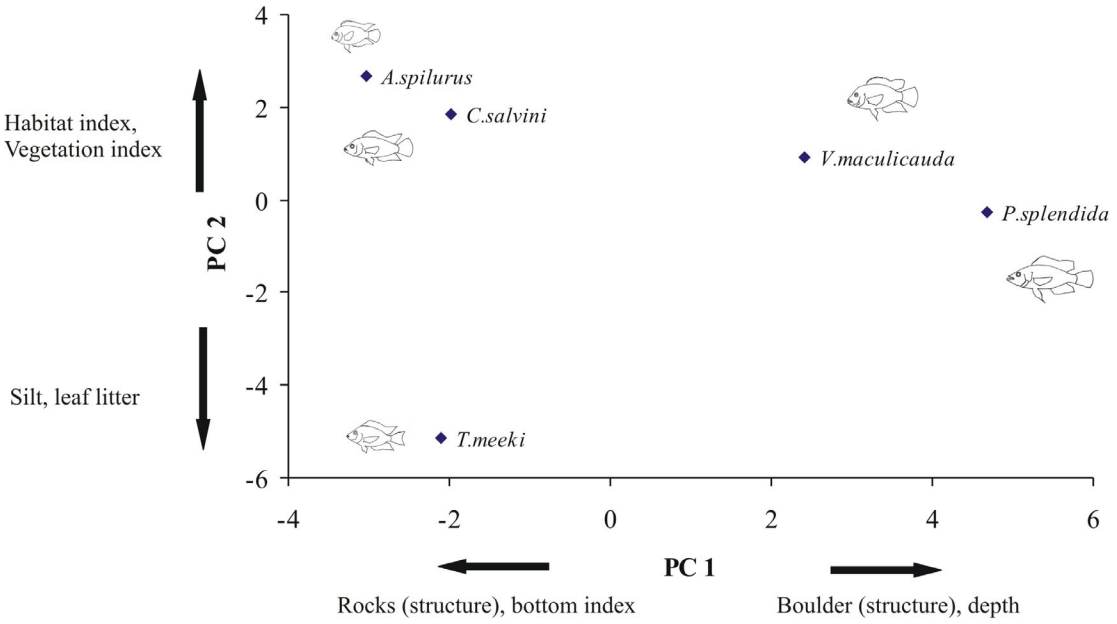
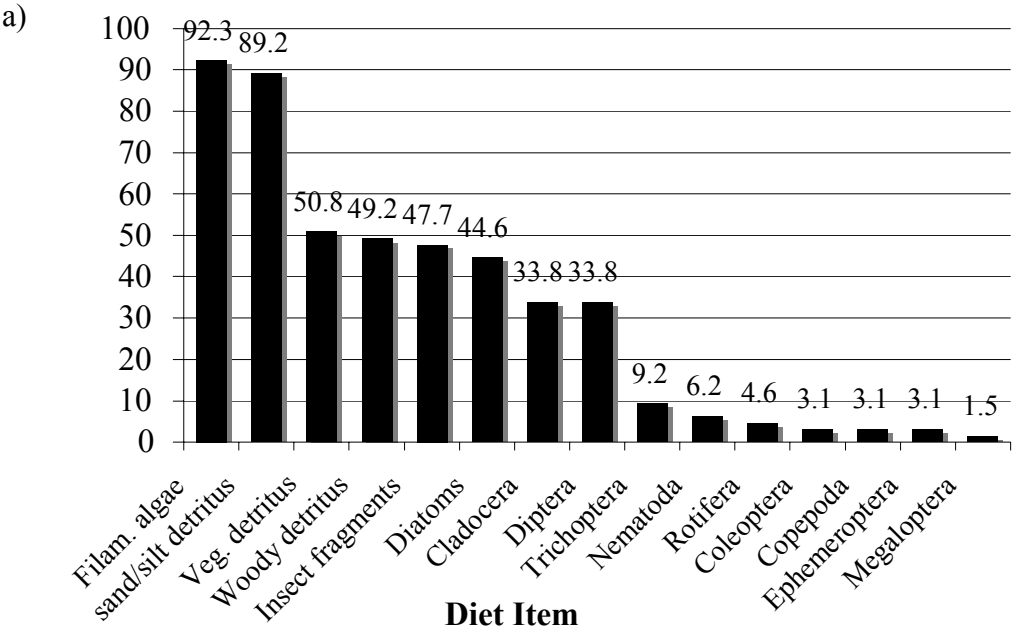


FIG.10 . Ordination plot of upper Bladen River cichlid species based on PCA of habitat variables for cichlid species in the upper Bladen River.

Archocentrus spilurus was the only herbivorous cichlid species, eating mostly filamentous algae (Fig.11 a, b.). Sixty-five stomachs were removed and dissected for analysis of stomach contents. Algae comprised 44 % of total volume and occurred in 93.2 % of all stomachs investigated. Sand and silt detritus, vegetative and woody detritus combined to make up 23.4 % of total volume and occurred in 89.2 %, 50.8 %, and 49.2 % of stomachs, respectively. It is likely that detritus was consumed while picking algae off of rocks, logs, and other structures. Invertebrates comprised a less significant portion of the diet. Miscellaneous unidentified insect fragments, as well as other microfauna, made up the remainder of the diet, however, no single item consisted of more than 2 % of the total diet volume. Although benthic insects were not a significant part of the diet volume, they sometimes were consumed along with algae removed from rocks, and these insects had a high frequency of occurrence in stomachs. Insect fragments occurred in 47 %, diatoms in 44.6 %, and cladoceran and diptera in 33.8 % of the stomachs examined.

a)



b)

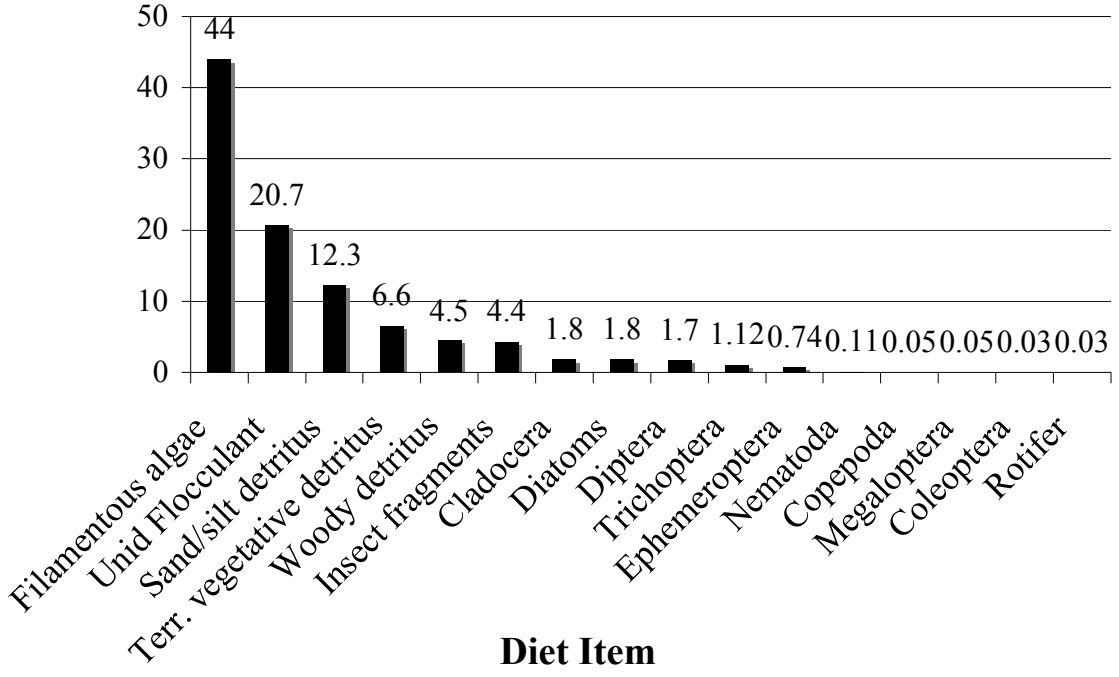
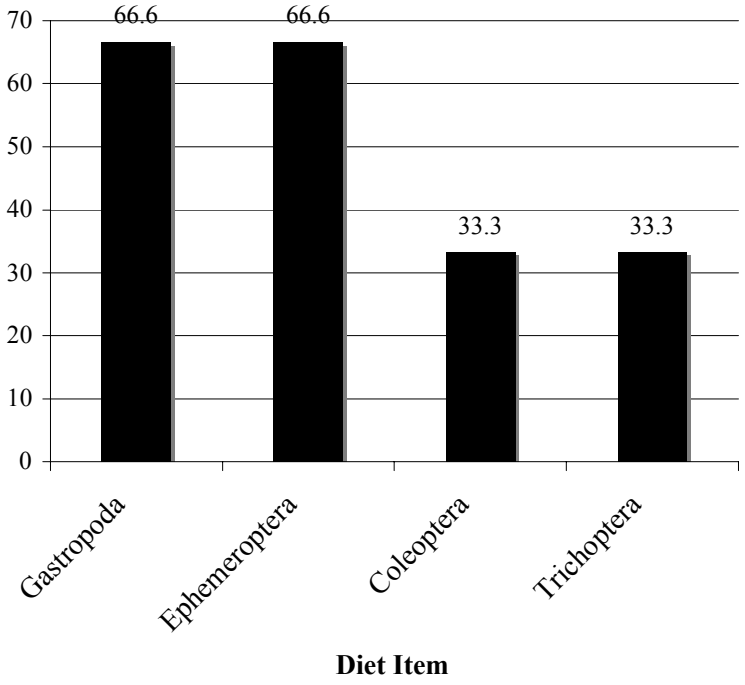


FIG.11. Diet of *A. spilurus*. *(a)* Each diet item as a percent of total diet volume; *(b)* frequency of occurrence of each diet item.

The stomachs of only three individuals of *A. robertsoni* were investigated (Fig.12). These individuals were collected in the study area during December of the previous year, and their stomachs were preserved in formalin. Although no *A. robertsoni* were collected during the sampling period in 2006-2007, they are included in the present study because they inhabit the region, albeit in low numbers (K.Winemiller, P.Esselmen, pers.com.). In terms of volume, the diet of *A. robertsoni* was dominated by aquatic insects and aquatic snails (62% and 38%, respectively). Most if the insects removed from *A. robertsoni* stomachs were Trichoptera (12%), Ephemeroptera (20%) and Coleoptera (30%). Snails and Ephemeroptera each occurred in 66% of the stomachs, whereas Trichoptera and Coleoptera were both present in one of three stomachs.

The only specialized piscivorous species of cichlid occurring in the Bladen River is *P. splendida* (Fig. 13). Among the 12 adult individuals that were collected, only eight had stomachs that contained food. Eighty-seven % of the total diet volume was fish, and 13% was comprised of shrimp. Half of the individuals with stomach contents had eaten fish, whereas 8.3% of the stomachs contained shrimp. Fish removed from stomachs were partially digested, and only small pieces of flesh and bones were recovered. Even though it was difficult to determine the specific identity of fish prey, numerous small teeth were present in two of the stomachs. Based on the size and morphology of these teeth, these fish were inferred to be juvenile *Astyanax aeneus*, a very abundant characiform in the upper Bladen River.

a)



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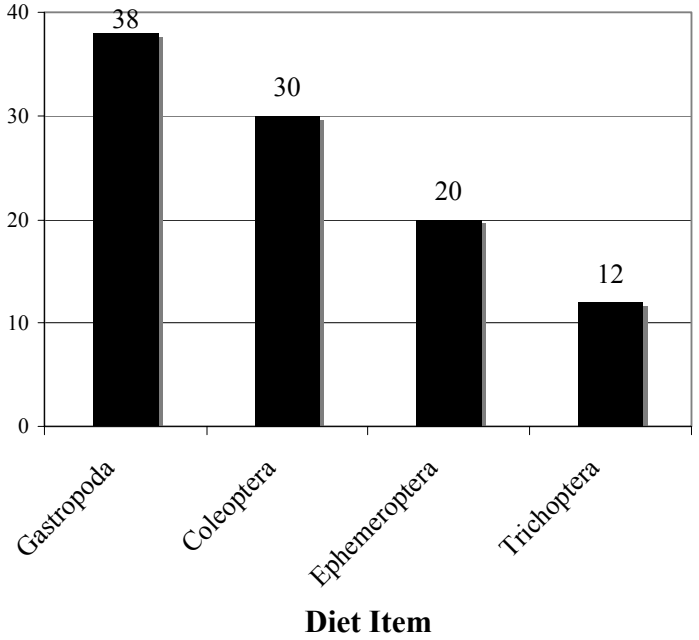
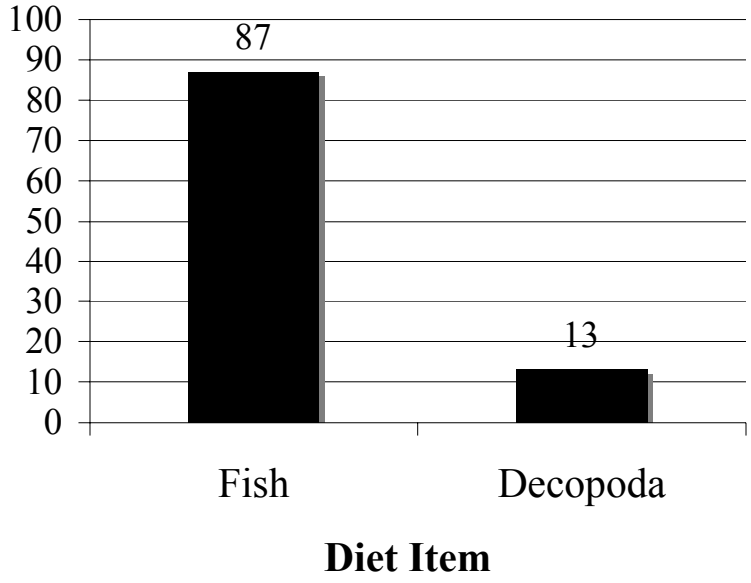


FIG. 12. Diet of *A. robertsoni*. *(a)* Each diet item as a percent of total diet volume; *(b)* frequency of occurrence of each diet item.

a)



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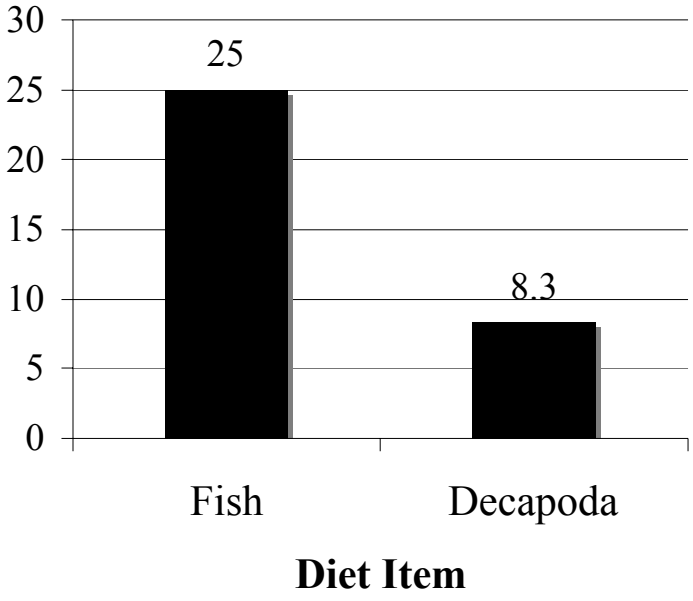
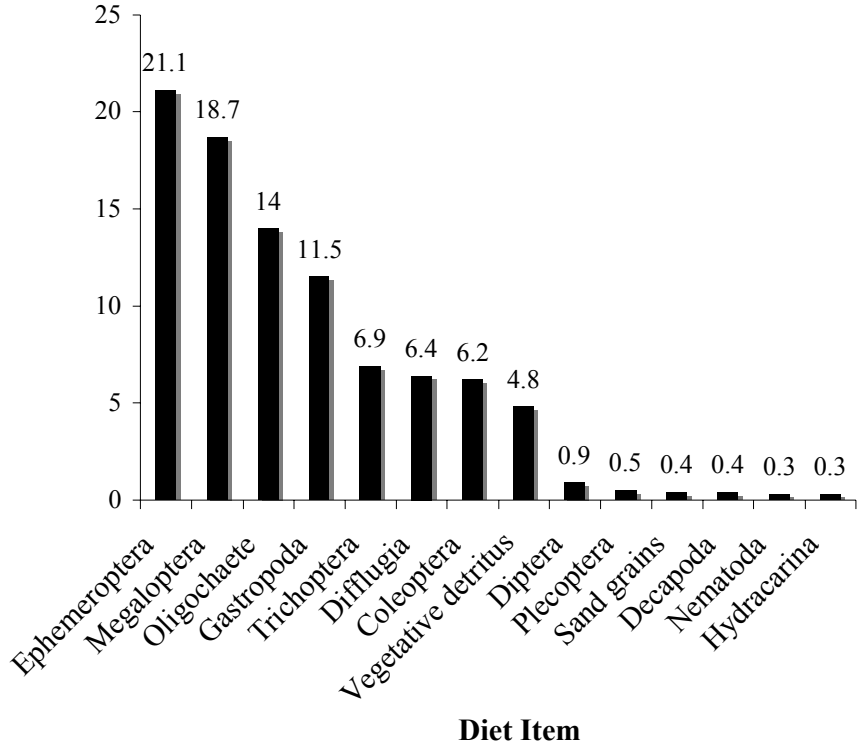


FIG.13. Diet of *P. splendida*. *(a)* Each diet item as a percent of total diet volume; *(b)* frequency of occurrence of each diet item.

Sixty-two stomachs of *C. salvini* were examined for contents (Fig. 14). Fourteen prey categories were found, including aquatic invertebrates, difflugiids, vegetative detritus, aquatic snails, Decapoda, Nematoda, and Hydracarina. Fifty-four % of the total volume was made up of Ephemeroptera, Megaloptera and oligochaetes (21.1 %, 18.7%, and 14%, respectively), and aquatic snails comprised 12.5% of the total volume. However, snails occurred at the highest frequency (41.1%), followed by Ephemeroptera (33.9%) and Trichoptera (25%).

Stomachs from 52 individuals of *T. meeki* were examined for gut contents (Fig.15). The diet of *T. meeki* was dominated by aquatic snails both in terms of volume and frequency (50.8% and 78.9%, respectively). The remaining volume was made up of aquatic insects, difflugiids, sand, vegetative detritus, Nematoda and Hydracarina. Of these, aquatic insects occurred with higher frequency and greater volume than the other types of diet items. *Thorichthys meeki* and *A. robertsoni* were the only species observed to consistently perform specialized substrate-sifting behavior while feeding.

a)



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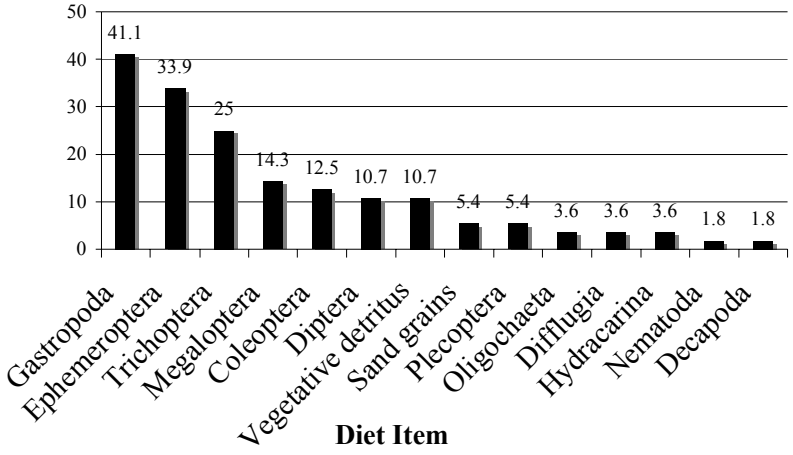
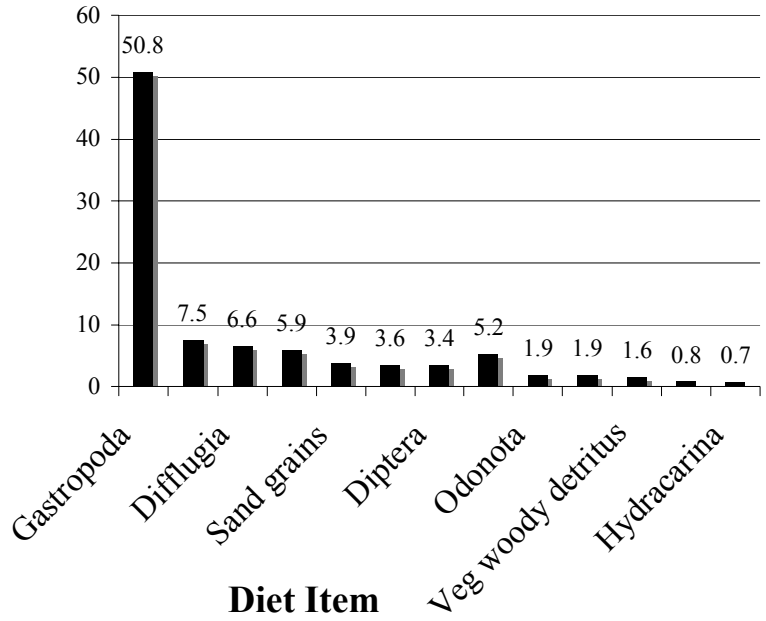


FIG.14. Diet of *C. salvini*. *(a)* Each diet item as a percent of total diet volume; *(b)* frequency of occurrence of each diet item.

a)



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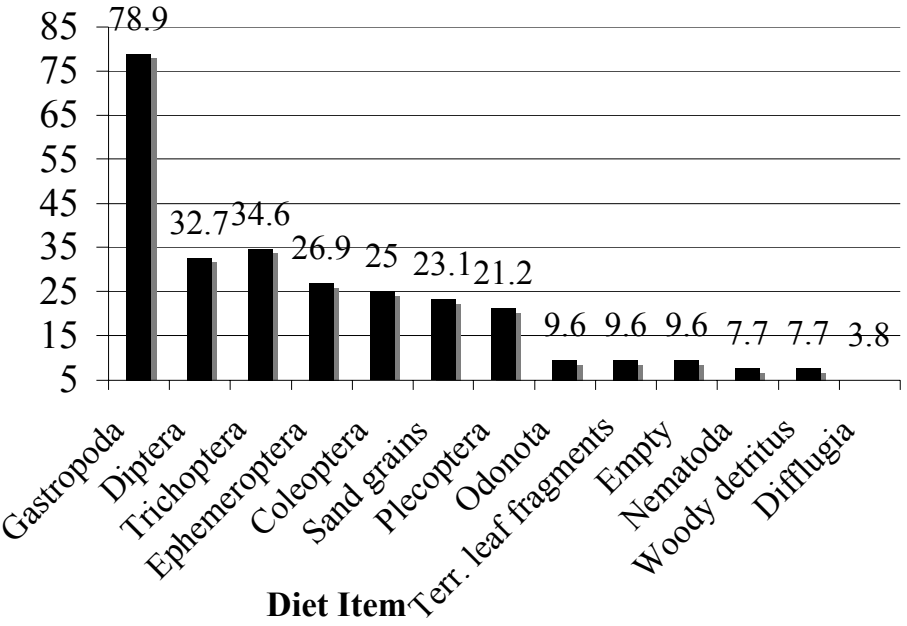
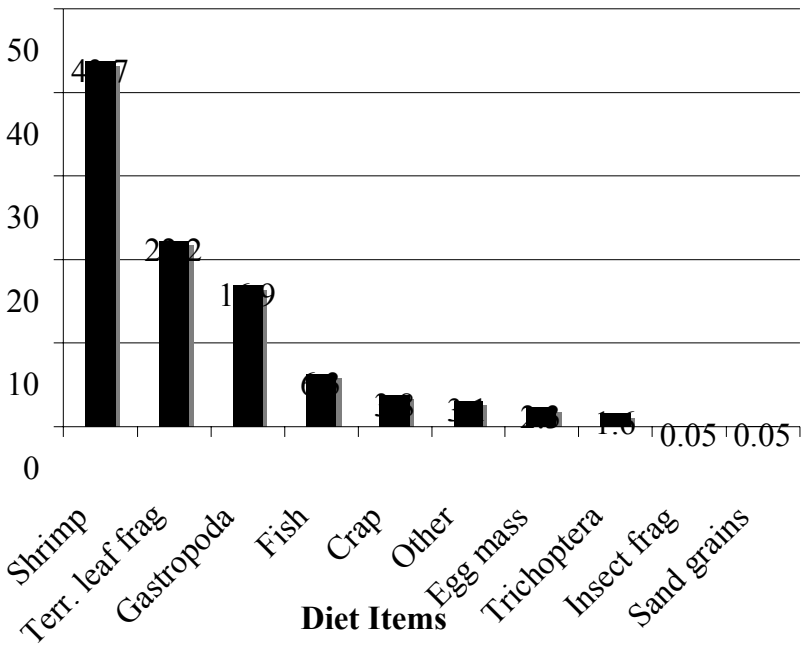


FIG. 15. Diet of *T. meeki*. *(a)* Each diet item as a percent of total diet volume; *(b)* frequency of occurrence of each diet item.

Twenty-three *V. maculicauda* were preserved for diet investigation (Fig.16). Major contributors to the total volume of stomach contents were shrimp (43.7%), leaf fragments (22.2%) and aquatic snails (16.9%). The remaining volume consisted of fish, crabs, invertebrate eggs, sand, and insect fragments. Aquatic snails occurred the most frequently (42.9%), followed by fish (33.3%) and shrimp (26.6%). Pectoral fin spines of a *Rhamdia guatemalensis* were found in one individual.

Principal components analysis of morphological variables of the six cichlid species resulted in the first three principal components (PC) axes explaining 83.9% of the total variance (38.9%, 26.6%, and 17.4% , respectively; Table 7, Fig.17). Inter-raker distance and snout length with mouth protruded were the two most positive loadings on the first axis (PC1). Head height and body depth were the two most negative loadings on PC1, indicating that greater inter-raker distance and snout length are associated with reduced relative head height and body depth.

a)



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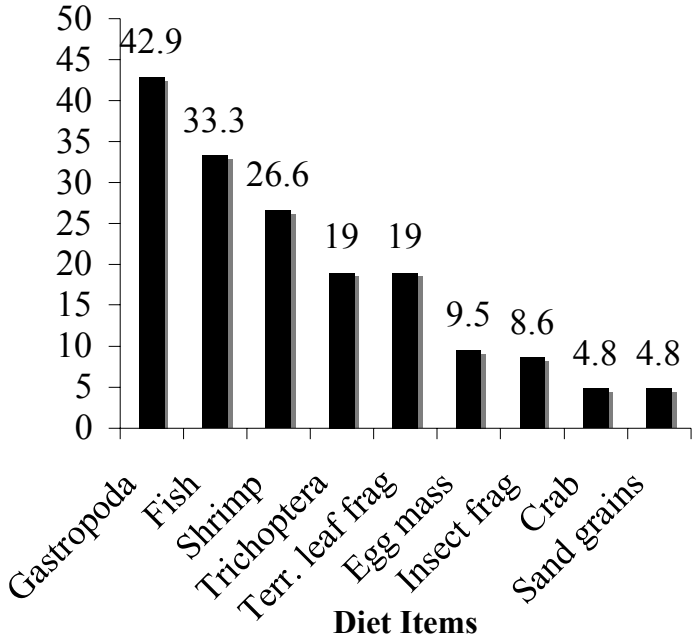

FIG. 16. Diet of *V. maculicauda*. *(a)* Each diet item as a percent of total diet volume; *(b)* frequency of occurrence of each diet item.

Species with high loadings on PC2 had longer ceratobranchials and shorter pharyngeal jaws, but greater gut length and shorter snout length with jaws closed. For PC3 (not shown), the variables with highest positive loadings were snout length with jaws closed and pelvic fin length, and highest negative loadings were for caudal peduncle depth and body depth.

Cichlasoma salvini and *P. splendida* grouped closely in morphospace as defined by PC 1 and 2, and were distinguished mostly by inter-raker distance and snout length with jaws open. *Archocentrus spilurus* was distinct from the other species in morphospace, and had a high loading corresponding to gut length and snout length when closed. *Vieja maculicauda* was separated from the other species by having high loadings on the first axis corresponding to relatively large head height and body depth. The morphospace occupied by *A. robertsoni* was associated with long ceratobranchials and lower pharyngeal jaw.

TABLE 7. Principle component analysis axis eigenvalues, proportion of variation modeled, and variable loadings from principal component analysis of Bladen River cichlid species based on averages of morphological characters.

	PCA axis			
	1	**2**	**3**	**4**
Eigenvalue	12.841	8.775	5.735	3.040
Proportion of variation	38.911	26.592	17.379	3.049
Cumulative variation	38.9	65.5	82.9	92.1
MSL	0.044	0.003	-0.029	0.264
HEAL	0.184	0.243	-0.062	0.015
HEAH	-0.267	0.062	0.037	-0.106
GAPE	0.192	0.212	0.127	-0.094
INTOR	-0.175	0.262	0.019	-0.020
EYEP	-0.185	0.241	0.020	-0.117
EYED	-0.010	0.248	0.133	0.325
SNTC	0.014	-0.204	0.327	-0.076
SNTO	0.236	0.096	0.156	-0.140
SNTTP	-0.127	0.122	-0.179	0.178
BODD	-0.265	0.036	-0.067	-0.123
BODW	-0.161	0.203	-0.220	0.056
PEDD	-0.225	0.029	-0.077	0.263
PEDL	0.023	0.266	0.115	-0.243
BDBM	-0.157	0.048	-0.024	-0.427
MOUPO	-0.254	-0.094	-0.090	-0.088
GUTL	-0.122	-0.247	-0.215	0.007
DORL	-0.239	-0.142	0.027	0.145
DORH	-0.205	-0.064	0.271	0.014
ANALL	-0.224	-0.121	0.160	-0.165
ANALH	-0.178	-0.133	0.256	-0.139
CAUDD	-0.081	0.032	-0.395	-0.019
CAUDL	-0.257	-0.078	-0.047	-0.167
PECTL	-0.007	0.254	0.236	0.184
PECTH	-0.026	0.280	-0.210	-0.083
PELVL	-0.136	0.124	0.317	-0.066
CERL	0.096	0.303	-0.034	-0.139
GILRN	0.044	0.003	-0.034	-0.139
INTRS	0.263	-0.064	0.020	-0.154
GILRL	-0.062	0.187	-0.275	-0.242
LPJW	-0.230	0.065	0.042	0.267
LPJL	-0.097	0.267	0.206	0.051
LPJD	-0.221	0.155	0.150	0.101

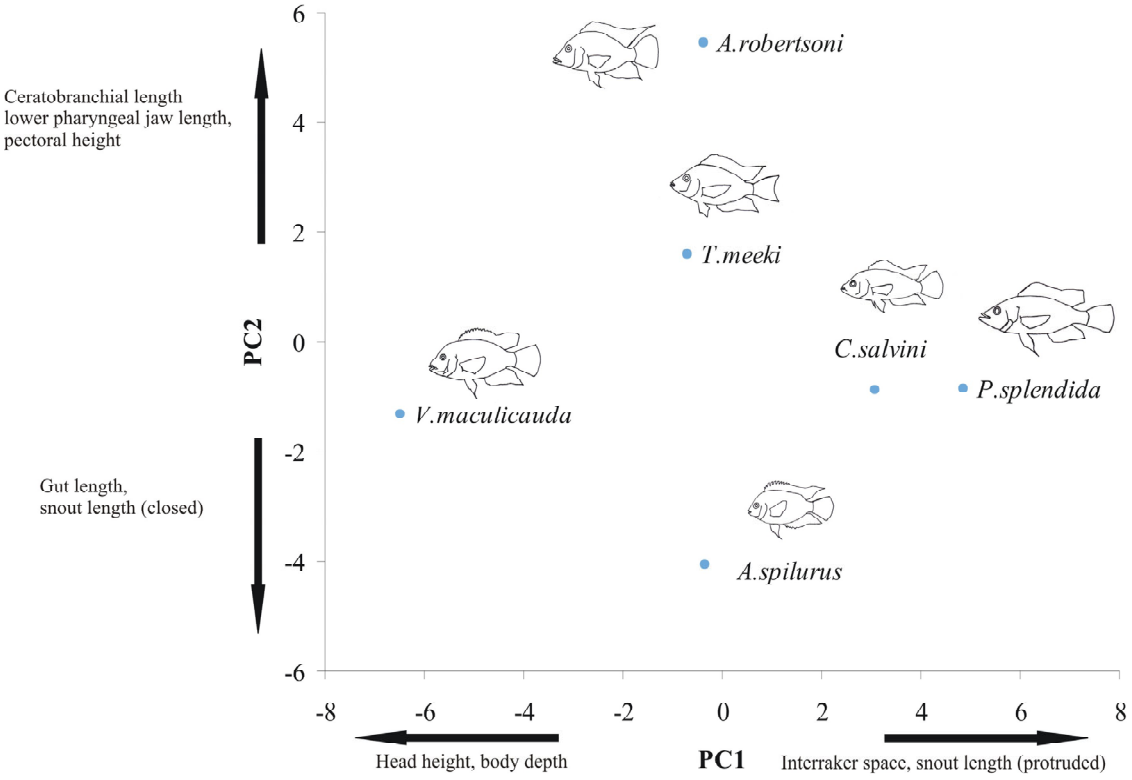

FIG.17. PCA ordination of Bladen River cichlid species based on morphological characters.

Ecomorphology

Relationships between diet and morphology among the cichlids of the upper Bladen River were explored using Canonical Correspondence Analysis (CCA), a direct gradient analysis technique that ordinates a set of observations (in this case species) by directly relating them to two series of associated variables (morphology and diet) (ter Braak 1986). CCA is a modification of Correspondence Analysis that adds a multiple regression step and simultaneously relates a primary set of variables (in this case diet) with the secondary variables (morphology), constraining the ordination so that scores represent the maximum correlation between diet and morphology. Orthogonal canonical axes are derived based on morphology, and express how well the morphological variables explain the variation in diet (ter Braak 1986; ter Braak and Smilauer 1998).

Before running the CCA, the number of morphological variables was reduced. Important variables related to feeding and swimming behavior were retained and manually tested for significance using forward selection. No variables were considered statistically significant, but nonetheless the analyses was completed because meaningful relationships can still be observed between diet and morphological variables (Table 8, Fig. 18).

TABLE 8. Canonical correspondence analysis investigating relationships between diet and morphology of *P. splendida*, *V. maculicauda, A. robertsoni. C. salvini, T. meeki,* and *A. spilurus.*

	CCA Axis	
	1	2
Eigenvalue	0.798	0.568
Diet-morphology correlation	1.000	1.000
Cumulative variation of diet-morphology relation	46.7	80.0
Sum of all unconstrained eigenvalues	1.708	
Sum of all canonical eigenvalues	1.708	
Monte Carlo tests of significance		
First canonical axis	Eigenvalue	0.798
	F-ratio	0.000
	P value	1.000
All canonical axis	Sum of eigenvalues	1.708
	F-ratio	0.000
	P value	1.000

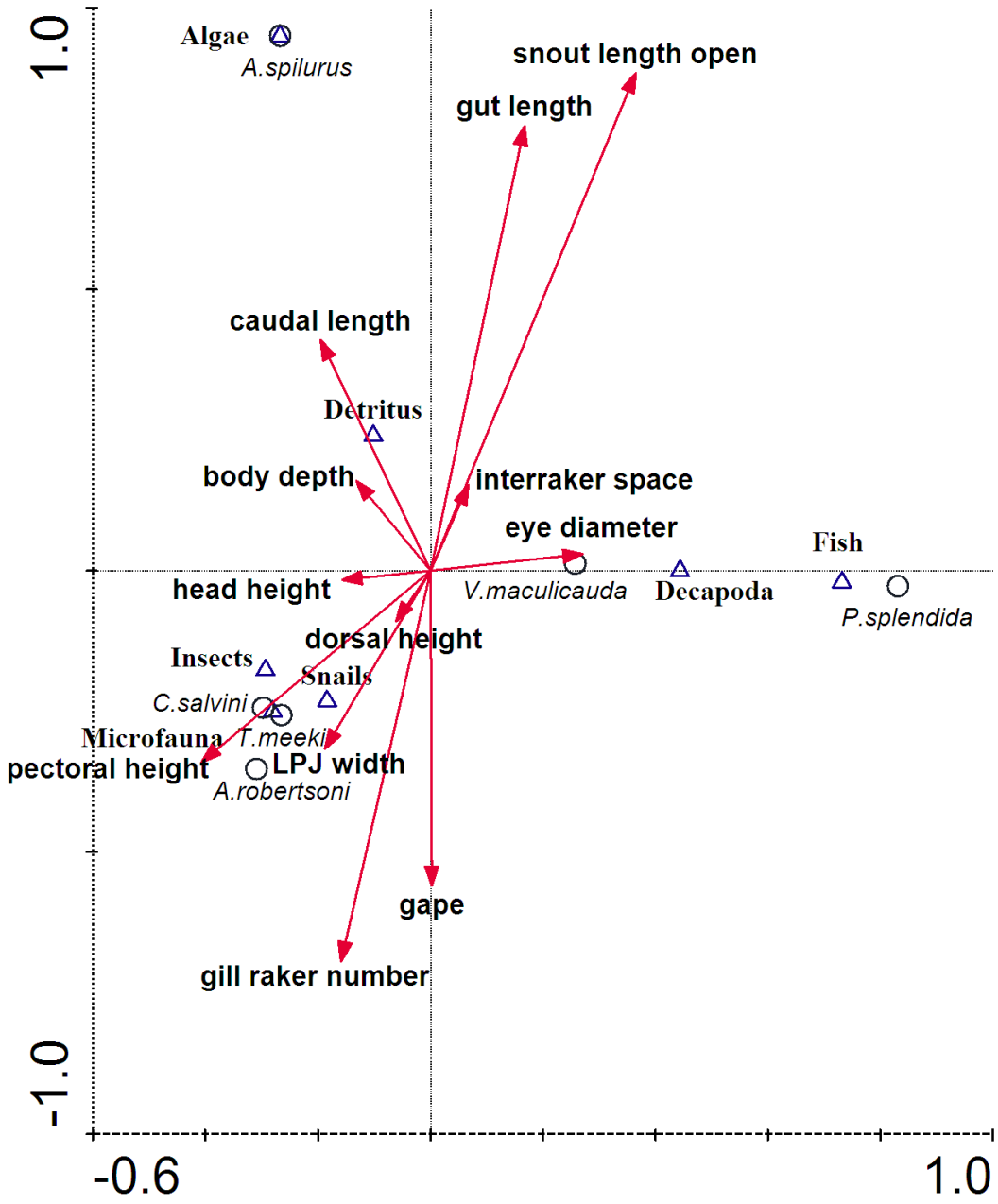

FIG.18. Ordination of canonical correspondence analysis of diet-morphology of *V. maculicauda, P. splendida, C. salvini, A. spilurus, T. meeki* and *A. robertsoni*.

Despite weak statistical relationships, this ordination does reveal trends in how diet variation is constrained by morphological attributes among the cichlids assemblage. The substrate sifters (*A. robertsoni* and *T. meeki*) were associated with a diet of invertebrates and microfauna and constrained by LPJ width, head height and pectoral fin height. *Archocentrus spilurus*, an algivore, was ordinated in close association with algae as well as gut length and snout length when open. The only predatory species, P. splendida, had a diet containing mostly fish, and constrained by eye diameter and intterraker space (Fig. 18).

When *P. splendida* was included in the CCA, the relationships between diet and morphology were not significant. This likely was due to *P. splendida* having extreme morphological attributes (e.g., snout length and standard length) compared to the other species. Thus, *P. splendida* was removed in order to model diet variation as constrained by morphological variation among the remaining cichlids in the assemblage. Only variables with P-values < 0.05 were retained in the final step of the analysis. Significant variables included gut length, eye diameter, and pectoral fin length. The CCA revealed a statistically significant relationship between diet and morphology along the first axis ($P=0.02$, $F= 0.926$, and eigenvalue $= 0.566$) (Table 9, Fig.19).

TABLE 9. Canonical correspondence analysis investigating relationships between diet and morphology of *V. maculicauda, A. robertsoni. C. salvini, T. meeki,* and *A. spilurus.*

	CCA Axis	
	1	2
Eigenvalues	0.566	0.490
Diet-morphology correlations	1.000	1.000
Cumulative variation		
of diet	48.1	89.7
of diet-morphology relation	51.2	95.6
Sum of all unconstrained eigenvalues	1.117	
Sum of all canonical eigenvalues	1.105	
Monte Carlo tests of significance		
First canonical axis	Eigenvalue	0.566
	F-ratio	0.926
	P value	0.020
All canonical axis	Sum of eigenvalues	1.105
	F-ratio	5.109
	P value	0.124

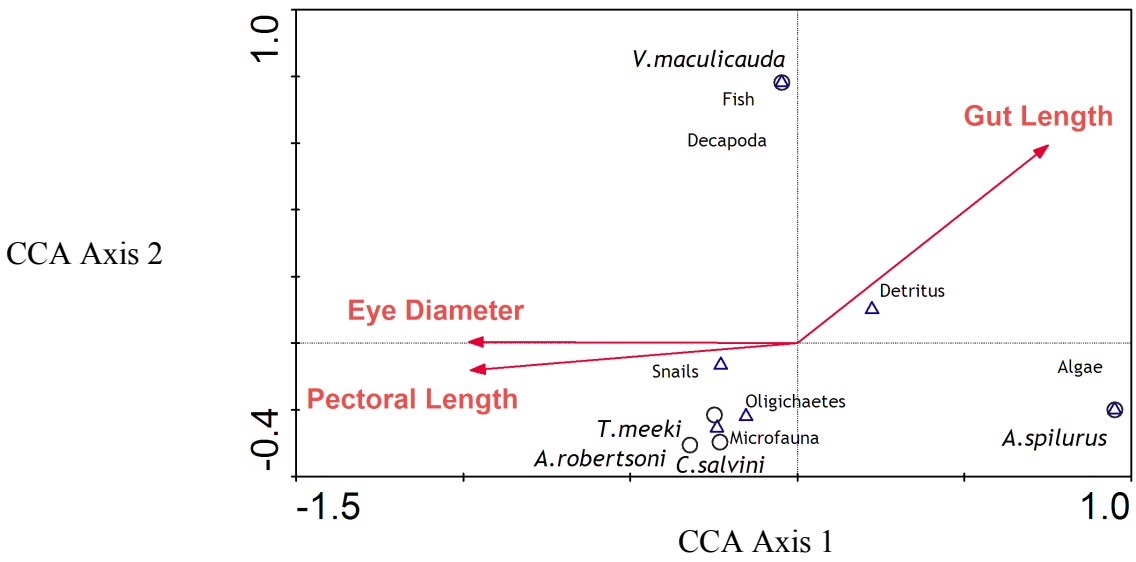

FIG.19. Ordination of canonical correspondence analysis of diet-morphology of *V.maculicauda, C. salvini, A. spilurus, T. meeki* and *A. robertsoni*

For the seven diet categories considered in this work, the fraction of variance explained by morphological variables ranged from 0.95 (algae) to 0.19 (micro fauna) (Table 10). For all diet categories, most of this variation was accounted for by the first axis. The first axis was positively correlated with gut length and positively associated with a diet dominated by detritus and algae and containing few invertebrates. Eye diameter and pectoral fin length were negatively correlated with axis 1 and associated with a diet of snails and other aquatic invertebrates.

With regard to the relative position of species and food items on the ordination diagram (Fig.19), species were divided into three broad categories: detritivores (*A. spilurus*), benthic feeders with a diet of snails and other aquatic invertebrates (*C. salvini, T. meeki, A. robertsoni)* and a generalist (*V. maculicauda*) whose diet contained fish, crustaceans, snails, and other invertebrates and detritus. Absent from the ordination is *P. splendida*, a predator, with a diet dominated by evasive prey including fish and decapods.

To determine how habitat use is constrained by morphological attributes, CCA was performed using morphology and habitat data. *Astatheros robertsoni* was removed from the CCA as it was not observed during habitat sampling (However, *A. robertsoni* was included in diet and morphological analyses, because it has been observed and collected in the study region and samples from sampling in December 2005 were obtained). Morphological variables with significant P-values were manually selected prior to the analysis. The CCA revealed a marginally significant relationship between habitat variables and morphology (P=0.056, F=3.126, eigenvalue = 0.013) (Table 11, Fig.20).

TABLE 10. Cumulative proportion of variance of the habitat categories explained by the first four axes of the CCA, and total percentage explained by the analysis.

CCA axis	1	2	% Explained
Algae	0.954	0.997	99.65
Detritus	0.672	0.809	84.24
Oligochaetes	0.251	0.769	95.56
Decapoda	0.003	0.995	99.98
Fish	0.003	0.995	99.98
Snails	0.739	0.800	93.15
Microfauna	0.187	0.396	47.77

TABLE 11. Canonical correspondence analysis investigating relationships between habitat and morphology of *P. splendida, V. maculicauda, C. salvini, T. meeki,* and *A. spilurus.*

		CCA Axis		
	1	2	3	4
Eigenvalues	0.080	0.047	0.004	0.011
Diet-morphology correlations	0.987	1.000	0.999	0.000
Cumulative variation				
of diet	56.6	89.9	92.5	100.0
of diet-morphology relation	61.2	97.2	100.0	0.0
Sum of all unconstrained eigenvalues	0.142			
Sum of all canonical eigenvalues	0.131			
Monte Carlo tests of significance				
First canonical axis	Eigenvalue	0.080		
	F-ratio	1.304		
	P value	0.306		
All canonical axis	Sum of eigenvalues	0.131		
	F-ratio	4.096		
	P value	0.138		

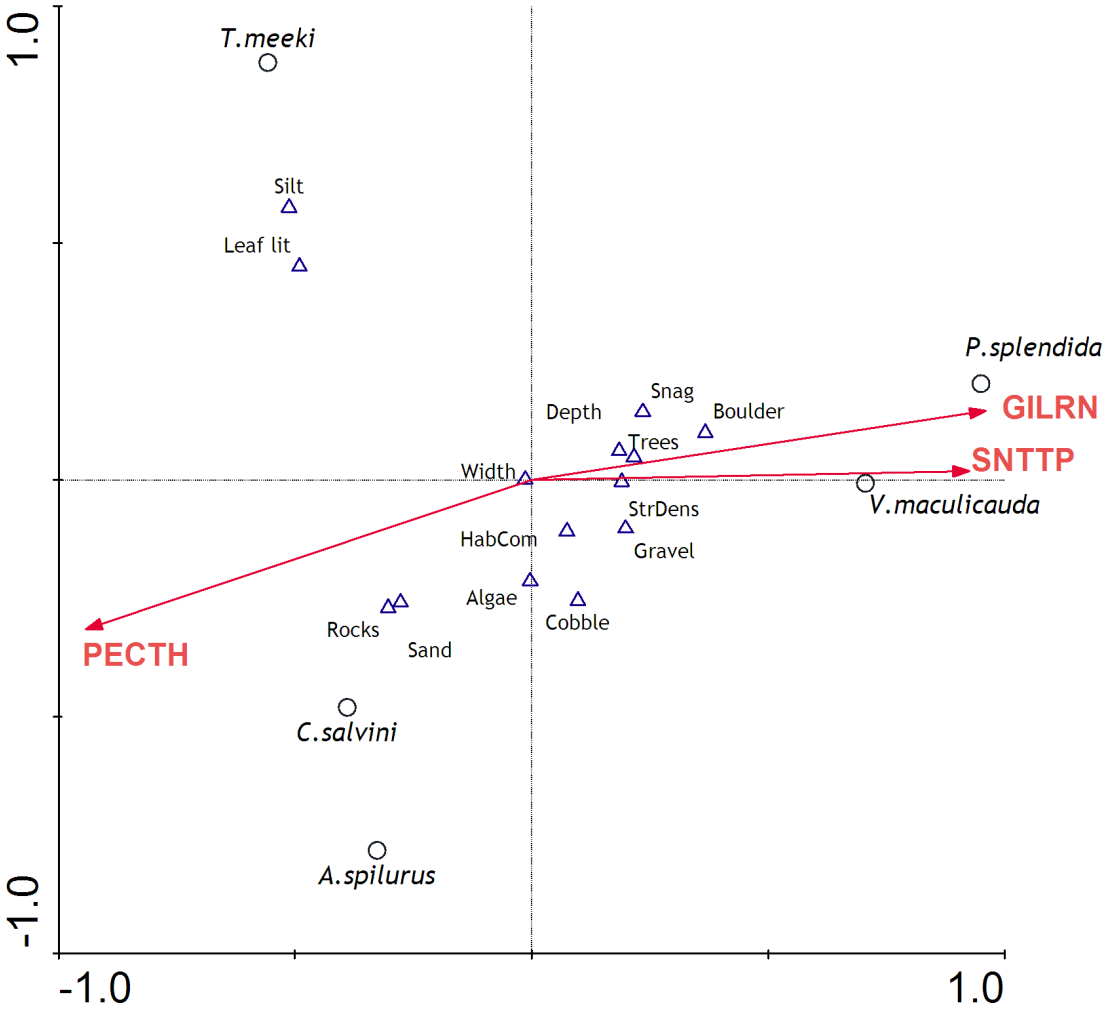

FIG.20. Canonical correspondence analysis ordination of species and habitat variables based on habitat-morphology relationships of *V. maculicauda, C. salvini, A. spilurus, T. meeki* and *P. splendida*.

For the habitat categories considered in this work, the fraction of variance explained by morphological variables ranged from 0.84 (rocks) to 0 (flow) (Table 12). For all habitat variables, the total variation accounted for by axes 1 and 2 was 98.7 and 1.3%, respectively. The first axis was correlated with gill-raker number and snout length with jaws protruded, and these features were associated with the presence of boulder and water depth. Pectoral height was negatively correlated with axis 1 and associated with the presence of rocks and sand.

With regard to the relative position of species and habitat variables in the ordination diagram (Fig.20), species divided into three broad categories: substrate sifters (*T. meeki*) associated with silty substrates, algae feeders (*A. spilurus*) and invertebrate pickers (*C. salvini*) associated with the presence of algae-covered rocks that supported attached aquatic invertebrates, and predators (*P. splendida*) associated with deeper waters and large boulders. In this multivariate analysis *V. maculicauda* was observed to be a habitat generalist and was not strongly associated with any particular habitat variable.

TABLE 12. Cumulative proportion of variance of the habitat categories explained by the first four axes of the CCA, and total percentage explained by the analysis.

CCA Axis	1	2	% Explained
Width	0.826	0.959	95.87
Depth	0.812	0.983	99.24
Flow	0	0.891	97.08
Algae	0.197	0.969	98.91
Bedrock	0.690	0.812	81.27
Rock	0.659	0.939	95.03
Cobble	0.003	0.866	87.92
Gravel	0.276	0.750	75.04
Sand	0.489	0.688	73.42
Silt	0.446	0.991	99.17
Leaf	0.532	0.979	97.91
Trees	0.034	0.113	91.18
Boulder (structure)	0.792	0.869	87.19
Rock (structure	0.838	0.993	99.77
Snag (structure)	0.071	0.270	75.31
Leaf (structure)	0.555	0.970	97.06
Structural density	0.279	0.280	30.10
Habitat complexity	0.117	0.973	99.60

Niche partitioning, niche overlap and morphological diversification

Pair-wise dietary niche overlap averaged 19.9 % and ranged from 0 to 80.8 % (Table 13). Highest overlap occurred between the two species of substrate sifters, *T. meeki* and *A. robertsoni* (80.8), followed by *A. robertsoni* and *C. salvini* (58.8). There was no overlap between *P. splendida* and *A. spilurus*, *T. meeki*, or *A. robertsoni*.

Standardized diet breadth (B_j) for consumer species averaged 0.43 and ranged from 0 to 1, indicating minimum and maximum niche breadth, respectively (Fig.21). *Astatheros robertsoni* had the highest value (0.82) indicating the highest diet breadth among the six cichlid species investigated. It should be noted, however, that stomachs from only three individual *A. robertsoni* were examined, so that the actually diet breadth is likely to be even greater. *Thorichthys meeki* had the lowest breadth (0.21), indicating that it is a dietary specialist. Over half of the total volume of diet of *T. meeki* consisted of aquatic snails.

TABLE 13. Dietary overlap (in percent) estimated using Pianka's (1974) index of symmetrical niche overlap.

	A. spilurus	*C. salvini*	*T. meeki*	*A. robertsoni*	*V. maculicauda*	*P. splendida*
A. spilurus	-	3.9	3.6	1.6	5.78	0
C. salvini	-	-	51.1	58.8	16.7	0.12
T. meeki	-	-	-	80.8	31.1	0
A. robertsoni	-	-	-	-	22.2	0
V. maculicauda	-	-	-	-	-	24.2
P. splendida	-	-	-	-	-	-

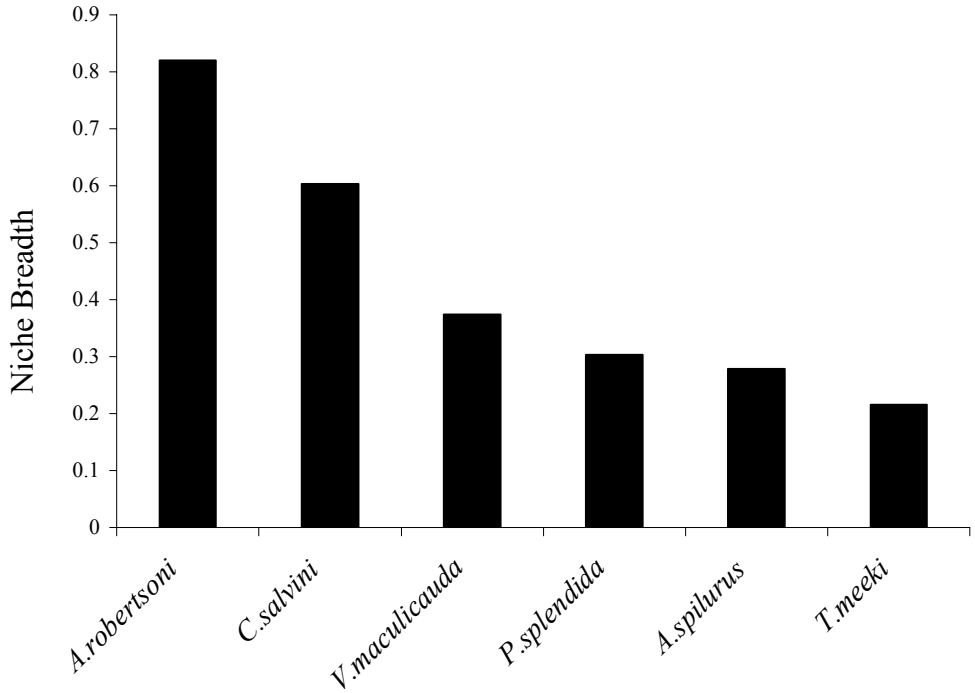

FIG.21. Dietary niche breadth calculated using Levin's measure (1968) and standardized with Hurlbert's method (1978).

A total of 712 cichlids was observed during snorkel surveys (Table 14). *Archocentrus spilurus* was observed 391 times, which constituted 55 % of all individuals counted. High counts of *A. spilurus* may have been due to conspicuous reproductive behavior, as brood-guarding pairs are highly territorial and not easily frightened by observers. Species habitat overlap was estimated with co-occurrence data and Jaccard's Index, with highest values indicating species pairs most frequently found together in the same habitat (Table 15). The highest overlap occurred between *V. maculicauda* and *C. salvini* (0.48) followed by *V. maculicauda* and *T. meeki* (0.4).

Among all species, values for dietary overlap were correlated with species co-occurrence using Spearman's rank correlation (Figure 22). The relationship was significant (2-tail, P= 0.028).

The pattern of dispersion of species in morphological space was determined by calculating the nearest-neighbor distance in Euclidean morphospace (Table 16). *'Cichlasoma' salvini* and *P. splendida* were closest (1.51), followed by *C. salvini* and *A. spilurus* (2.68). The greatest morphological distance was between *V. maculicauda* and *P. splendida* (3.38).

Thorichthys meeki was closest to the morphological centroid (0.45), followed by *C. salvini* (0.85). This implies that these species have the most generalized morphologies within the species assemblage.

TABLE 14. Summary of species' local abundances estimated from snorkel surveys.

Species	Observed (n)	% of total (%)
A. spilurus	391	54.9
V. maculicauda	131	18.4
T. meeki	106	14.9
C. salvini	70	9.8
P. splendida	14	2
	n=712	100.0

TABLE 15. Frequency of co-occurrence and Jaccard's Index (J) of habitat overlap among cichlid species censused during snorkeling surveys in the upper Bladen River, Belize.

	(Co-occurrence of both species / Jaccard's Index)						
	Frequency of occur-ence (59 pts)	*A. spilurus*	*C. salvini*	*T. meeki*	*V. maculicauda*	*P. splendida*	Mean
A. spilurus	45	-	18 / 0.39	13 /0.27	16 / 0.33	3 / 0.07	0.26
C. salvini	19	-	-	9 / 0.33	12 / 0.48	2 / 0.10	0.325
T. meeki	17	-	-	-	10 / 0.40	3 / 0.17	0.293
V. maculicauda	18	-	-	-	-	4 / 0.22	0.356
P. splendida	4	-	-	-	-	-	0.140

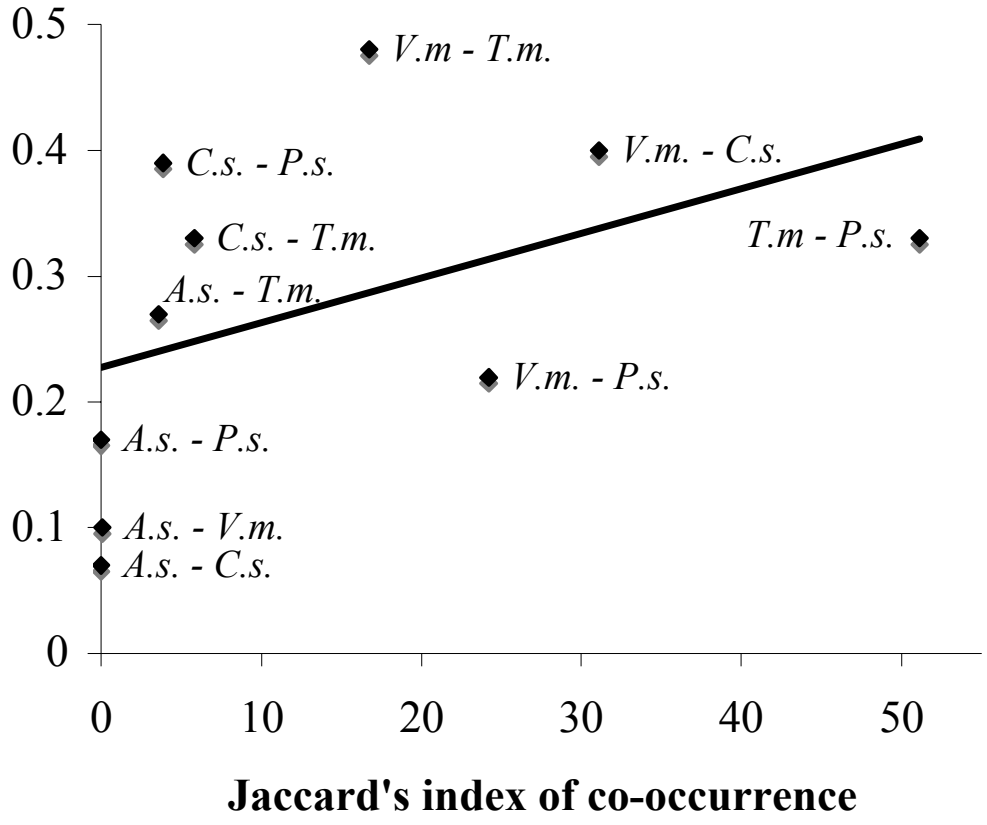

Figure 22. Linear regression of dietary overlap and co-occurrence.

TABLE 16. Nearest-neighbor Euclidean distance in morphospace and mean distance to the morphological centroid for upper Bladen River cichlid species.

	Average distance to the centroid	*A. robertsoni*	*A. spilurus*	*C. salvini*	*T. meeki*	*V. maculicauda*	*P. splendida*
A. robertsoni	0.89	-	3.14	2.95	**2.93***	3.14	2.96
A. spilurus	2.14		-	**2.68***	2.97	**2.93***	2.69
C. salvini	0.85			-	**2.69**	3.14	**1.51***
T. meeki	0.45				-	2.95	2.76
V. maculicauda	1.01					-	3.38
P. splendida	1.86						-
Average nearest-neighbor distance (NND)	2.38						

***nearest neighbor**

DISCUSSION AND SUMMARY

The purpose of this study was to investigate relationships of morphology, habitat use and diet within an assemblage of cichlids in the upper Bladen River, Belize. This assemblage was expected to demonstrate a relatively high degree of niche divergence and resource partitioning when compared with similar studies of temperate stream fish communities, but perhaps less ecological specialization when compared to more diverse cichlid assemblages, such as those in the lowlands of the Rio Usumacinta Basin in Mexico or Rio San Juan Basin in Costa Rica. Because the upper Bladen River lies within a protected area, this location provided a relatively pristine location for field research.

Principal components analysis of morphometric data indicated that species separated by a variety of characters associated with feeding and microhabitat utilization (Fig.17). The first axis separated the predator (*P. splendida*) and invertebrate feeder (*C. salvini*) from the remaining species by narrow body, wider inter-raker space, and a longer snout length. Having fewer gill rakers is a trait linked with piscivory, wheras the long snout of *P. splendida*, and to a lesser extent *C. salvini*, should be associated with enhanced suction feeding. Suction feeding is one of two main feeding modes observed in cichlids (Barel 1983). Suction involves rapidly opening the mouth as well as a premaxillary protrusion (Fig. 23), causing an increase in buccal volume. Negative pressure generated inside of the mouth leads to the creation of a jet of water that drags prey into the mouth (Norton and Brainerd 1993, Norton 1995). Other studies have linked fish with large mouths to consumption of larger, more evasive prey. Higham et al. (2006) found that 96 percent of *P. splendida*'s diet contained evasive prey, and linked this diet to having a large gape and high ram speed during prey capture.

An alternative mode of feeding observed in cichlids is biting. Efficient biting compromises suction feeding because it is associated with both reduced protrusability and mouth volume (Barel 1983, 1993). Due to conflicting mechanical demands of various morphologies, a trade-off exists between these two strategies. In other words, a fish cannot optimally employ both biting and sucking modes of feeding (Barel 1983, de Visser and Barel 1996).

The remaining species, including *V. maculicauda, A. spilurus, A. robertsoni* and *T. meeki,* are deep bodied, a trait associated with the ability to maneuver in a vertical plane. This ability is important for *A. spilurus* in maneuvering among rocks where it feeds on periphyton, and for *A. robertsoni* and *T. meeki* in substrate sifting over soft sediments. Additionally, the high maneuverability associated with a deep body would be adaptive for *V. maculicauda*, a generalist feeder with a diet containing fish, crustaceans, molluscs, detritus and invertebrates.

Fig. 23. Extreme snout protrusion observed in *Petenia splendida* (photo by Jennifer Cochran).

The second PCA axis was influenced by characteristics related to substrate sifting including ceratobranchial length and lower pharyngeal jaw length (Fig.17). These two characteristics of the pharyngeal apparatus separated the substrate sifters, *A. robertsoni* and *T. meeki*, from the other cichlid species. The pharyngeal jaw is of particular interest in cichlid ecology, because evolved changes in this apparatus are believed to have led to the extensive trophic diversification of this family. In many bony fishes, the pharyngeal apparatus is the primary location of prey processing prior to entry into the gastrointestinal tract. Food items often are sheared and fragmented during winnowing within the orobranchial chamber, and modifications of the pharyngeal jaws partially determine what types of food a fish can exploit (Liem 1973, Wainright 1989, Drucker and Jensen 1991, Grubich 2003). *Astatheros robertsoni* and *T. meeki* have longer ceratobranchials and lower pharyngeal jaws, and also have diets dominated by aquatic macroinvertebrates, including snails that are sifted from the substrate (Figs 12, 15). Fusion of the cichlid pharyngeal jaw and hypertrophy of the associated muscular sling is associated with enhanced ability to crush shelled molluscs and other hard prey (Hulsey 2006).

Many studies have found morphological diversification and specialization in stream fishes to be associated with diet and microhabitat use (Gatz 1979, Moyle and Senanayake 1984, Winemiller 1991). In the Bladen River, cichlids tended to be associated with pool and edge habitats that contained low flow and physical structure, such as woody snags, boulders and rocks (Table 5, Fig. 10).

Whereas other studies have associated cichlids with highly vegetated habitats (Winemiller and Leslie 1992), other Neotropical riverine habitats offer only seasonal macrophyle growth (Soares et al. 1986) but the only aquatic vegetation found in this

stretch of the Bladen River was filamentous algae. A comparison of the diet of *V. maculicauda* from a vegetated Río Tortuguero in Costa Rica with the present study in Belize reveals significant trophic differences. Winemiller et al. (1995) found over 75 % of *V. maculicauda*'s diet to contain detritus and algae in the Tortuguero drainage, whereas in the Bladen, *V. maculicauda*'s diet contained freshwater shrimp (43.7 % total volume), leafy detritus (22.2 %) and snails (16.9 %) (Fig.16). A fin spine from a juvenile catfish, *Rhamdia guatemalensis*, was also found in one stomach, and 6.3 % of the total volume of stomach contents was made up of fish pieces. The lower pharyngeal jaw of this species contains both molariform and papilliform teeth, and reflects an ability to process a variety of prey types (Fig. 24). Molariform teeth allow for crushing hard items like molluscs, and papilliform teeth can be used to process softer prey with less force (Hulsey 2006). The pharyngeal jaw of *A. spilirus* contained papilliform teeth, and this species had a diet consisting mostly of algae and detritus. Other studies have found the jaw morphology of cichlids to be an example of a trophic polymorphism, in which two or more different phenotypes occur in a single species and will influence feeding performance (Wainright 1996, Husley et al. 2005). Polymorphism associated with feeding behavior was not observed in any of the upper Bladen River cichlids.

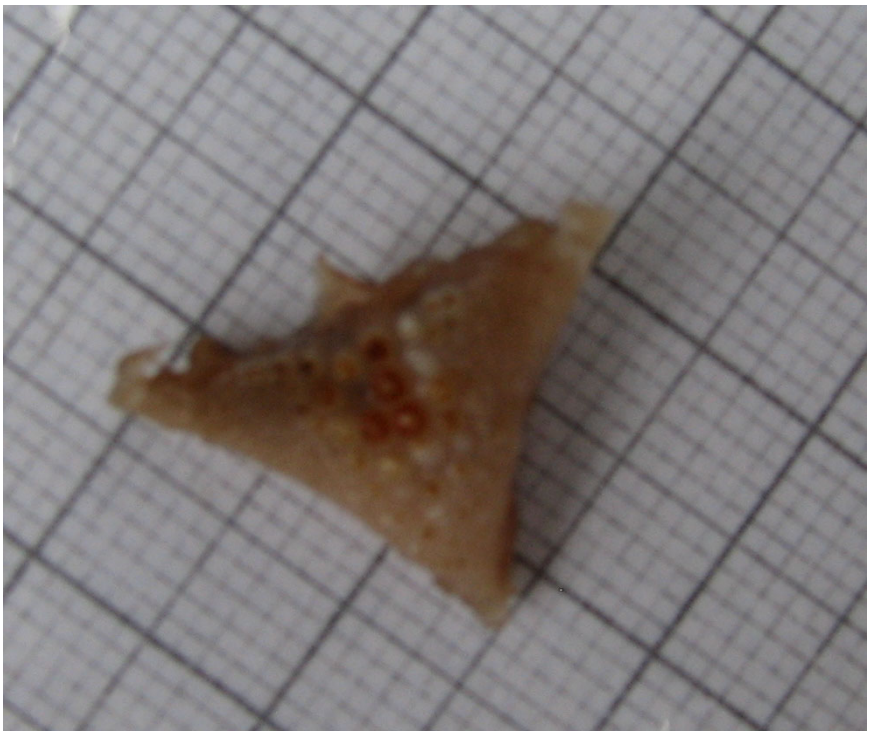

Fig.24. Lower pharyngeal jaw of *V. maculicauda* featuring molariform teeth (photograph by Jennifer Cochran).

Multivariate statistics also were used to investigate relationships between habitat use and morphology. A canonical correspondence analysis associated *A. spilurus* and *C. salvini* with long pectoral height, and found both species associated with habitats containing rocks and algae (Fig.20). In addition to aiding acceleration, long pectoral fins should allow for efficient maneuvering around rocks where the major food resources of these species occur. Species that frequent rocky substrates use the opening among rocks for cover from predators and for protective spawning surfaces. Other fish that are too large are physically excluded from these habitats, and in the Bladen River these included *V. maculicauda* and *P. splendida*. These larger species were more often associated with deeper water and large boulders (Fig.10).

In addition to maintaining position among rocks, long pectoral fins also aid in maintaining balance and stability while maneuvering within current. *Archocentrus spilurus* was often observed biting at rocks in the middle of long shallow runs where the current velocity was relatively high. Algae, the dominant food source of *A. spilurus*, were found growing on the rocks, and several families of aquatic invertebrates, important in the diet of *C. salvini*, were found attached to the underside of rocks. Consistent with findings from the PCA, the CCA distinguished *P. splendida* based on possession of a long snout, highly protrusible jaws, and a large inter-raker space. A piscivore that uses suction feeding, *P. splendida* was often observed in deep pools where large structure was present (Fig.10). Although the CCA did not yield statistically significant associations between morphological attributes and habitat features for *T. meeki* and *A. robertsoni*, these species were associated with habitats containing silt and leaf litter, which are substrates suitable for digging and sifting. The PCA ordination of habitat did associate

these substrate sifters with silt and leaf litter (Fig. 10). Other studies have also highlighted that fish associated with soft substrates are strongly influenced by water depth and the nature of the substrate (for examples see Lewis 1981, Lowe-McConnell 1987).

Neotropical cichlids associated with slow moving waters of floodplain rivers and slow-moving creeks and have several characteristics that enable exploitation of lentic habitats. First, all cichlids have a completely enclosed air bladder capable of secreting gases that allow them to maintain a constant bladder volume regardless of depth (Lowe-McConnell 1969). Additionally, lentic-adapted cichlids have broad pectoral and caudal fins that allow them to fan water, which helps bring oxygen to eggs in hypoxic areas away from the current. Broad pectoral and medial fins also facilitate precise movements around rocks and other structures (Zaret 1980).

In addition to exploring relationships between morphology and habitat use, I also investigated how diet is associated with morphometric traits using CCA (Figs 19, 20). In order to extract significant relationships among the cichlid species, *P. splendida* was removed from the analysis because of extreme morphological characteristics that prevented significant results from the analysis. The CCA results showed diet to be significantly associated with eye diameter, pectoral fin length and gut length. A large relative eye diameter was positively associated with snails and microfauna in the diets of *C. salvini*, *T. meeki*, and *A. robertsoni*. Gatz (1979) interpreted eye size to reflect the importance of vision in feeding. Digestive tract length was positively associated with algivory and detrivory as exemplified by *A. spilurus*. A similar pattern was observed in African cichlids (Fryer and Iles 1972) and African fishes in coastal lakes of Benin (Adite

and Winemiller 1997). Pectoral fin length was associated diets containing large proportions of snails and microfauna as observed in *T. meeki*, *A. .robertsoni* and *C. salvini*.

The major food sources of Neotropical riverine cichlids include fish, molluscs, crusteaceans and aquatic invertebrates (especially juvenile stages of aquatic insects), aquatic macrophytes, algae and detritus. Many species that contain a broad range of diet items, however, seem to prefer foods for which they are best adapted (Lowe-McConnell 1991). Some species pairs with similar trophic adaptations, also consumed similar food sources. Highest dietary overlap occurred between *A. robertsoni* and *T. meeki* (80.8%). Both species are substrate sifters and had diets containing predominately aquatic snails (Figs. 12, 15). Analysis of stomach contents revealed that most snails were crushed in the anterior portion of the gut, but others remained in tact throughout the digestive system. Intact snail shells were between 1.5 and 3.0 mm in length and approximately 0.5-1.0 mm wide. *Astatheros robertsoni* also consumed aquatic snails and had 58.8% dietary overlap with *C. salvini* (Table 13). In addition to snails, both species consumed aquatic insects including representatives Coleoptera, Ephemeroptera and Trichoptera. Even though there was considerable dietary overlap between several of the cichlid species, this does not necessarily indicate the existence of resource competition. High niche overlap may reflect a high availability of resources that exceeds demand by consumers (Ross 1986), or may result when niche partitioning takes place based on discrimination of resource states at a finer scale of resolution than the one used in the analysis.

Although aquatic snails were prevalent in many fish stomachs and visibly abundant throughout the study area, they may be a seasonally abundant food resource in the Bladen River. Other studies of heroine cichlids have described morphological specializations for molluscivory in the Cichlidae. Hulsey (2006) reported 12 of 32 Mesoamerican heroine species to have gut contents containing more than 5 % molluscs by volume, and established a clear relationship between greater pharyngeal suturing and molluscivory among evolutionary disparate lineages of heroine cichlids. The present study in the Bladen found molluscs in the diets of four of six cichlid species with volumes ranging from 11.5% (*C. salvini*) to 50.8% (*T. meeki*). There are three common snail species in the upper Bladen River: *Pachycheilus largillierti*, *Pachycheilus corvinus*, *Melanoides tuberculatus* (Fig. 25). *Pachycheilus corvinuswas* was encountered in many cichlid stomachs. According to local naturalists (Dan Dourson, personal communication), this species is a fall breeder that deposits masses of gelatinous eggs under rocks in the river. By the beginning of the dry season in December and January, the snails hatch and are prevalent in the substrate. The hatchlings are approximately 4 to 6 mm in length and are estimated to reach adult size by the summer. Most aquatic snails, including the ones in the Bladen, feed on the algae that grow on various substrates in the river including but not limited to rocks, submerged logs, and submerged forest debris (Dan Dourson, personal communication).

Fig. 25. Three species of aquatic snail found in the upper Bladen River: (a) *Pachycheilus largillierti*; (b) *Pachycheilus corvinus*; (c) *Melanoides tuberculatus*, an introduction from southeast Asia (photograph by Dan Dourson).

In theory, niche differences cause species to limit their own population growth more than others, thereby promoting coexistence (Chesson 2000). *Astatheros robertsoni* had the greatest niche breadth (0.82) indicating that this species used the broadest range of food resources (Fig.21). *Thorichthys meeki* had the lowest value (0.21), and over half of the total volume of food removed from stomachs consisted of aquatic snails (Figs 15, 21). Both of these species are substrate sifters, and *T. meeki* was most often observed and collected in the presence of silt, mud and leafy substrates (Table 5, Fig.10). Aquatic snails usually were embedded within the substrate, and were consumed along with other benthic invertebrates. In addition, the niche breadth indicates that *V. maculicauda*, *P. splendida*, and *A. spilurus* had more specialized diets, however, similar to estimates of dietary overlap, this index also can be biased from coarse taxonomic resolution of resource categories.

Jaccard's Index was used to measure co-occurrence of species using data collected during the snorkeling observations. The highest frequency of species co-occurrence was between *V. maculicauda* and *C. salvini* (0.48) followed by *V. maculicauda* and *T. meeki* (0.40) (Table 15). The cichlid species that least frequently co-occurred in habitats with other cichlids was the predatory cichlid, *Petenia splendida*, (0.14) (Table 15). The next lowest value for co-occurrence occurred between *A. spilurus* and *T. .meeki* (0.27), a pattern that probably was influenced by the territorial behavior of breeding pairs. *Archocentrus spilurus* was the only cichlid species regularly observed in shallow run reaches containing moderate to swift current velocities.

Pair wise values for species co-occurrence and diet overlap were positively correlated (Fig. 22). This relationship does not suggest niche complementarity in which pairs of species with high dietary overlap have low overlap in habitat use, and species

with overlap in habitat use have low dietary overlap. Instead, it suggests that species are responding similarly to spatial variation in food resource availability according to habitat units.

Species that occupy the same habitats may have similar morphology in response to adaptation to the physical environment (Grant 1972), or they may have divergent morphology in response to interspecific competition (Brown and Wilson 1956, Hutchinson 1959). Only a few morphological traits were significantly associated with patterns of food resource and habitat use by Bladen River cichlids. This failure to identify more extensive correlations between morphology, diet and habitat may not be entirely surprising. Ecomorphological relationships can be confounded by a variety of factors related to behavior, physiology, ecology and morphology (Motta and Kotrshal 1992). A limitation of the ecomorphological approach is that morphology, just like physiology and behavior, does not necessarily respond to varying environmental conditions during ontogeny. Also, morphological traits and measurements may have multiple functional roles and implications with different ecological relationships for different species.

Another potential limitation of the ecomorphological analysis involving the local cichlid assemblage is that cichlid morphospace may be influenced by the non-cichlid species found in the upper Bladen (e.g., *Rhamdia guatemalensis*, *Gobiomorus dormitor, Awaous banana*, *Xiphophorus helleri*, *Astyanax bimaculatus*). Despite limitations such as this, ecomorphological investigations are especially important in tropical areas where the niche relationships of many fish species are poorly documented. This approach can aid in predicting patterns of resource use, which in turn will assist in biodiversity

conservation. The present study has revealed that fish feeding, and to a lesser extent habitat use, may be predicted from a few morphological attributes.

Patterns of ecological specialization tend to be more difficult to identify among river fishes, because flooding cycles alter the availability of resources as well as ratios of consumer supply and demand (Winemiller 1989, 1990). Seasonal resource availability may strongly influence diet, and in the present study only one season was considered. Often, resource specialization and niche partitioning among river fishes is apparent only in relation to several seasonal cycles, and such investigations require extensive field sampling and examination of many individuals.

Overall, the present study provides evidence of habitat and diet partitioning among cichlids inhabiting the Bladen River. As Liem (1991) proposed, feeding specializations seem to be expressed only during certain periods of the year when food is limited. Interspecific interactions can only be fully estimated by examining patterns of resource use over extended periods, preferably encompassing a full annual cycle. Nonetheless, the present study revealed patterns of trophic and morphological diversity consistent with a hypothesis of resource partitioning in accordance with adaptive divergence in morphological traits that influence ecological performance. The Bladen cichlid assemblage has one algivore with a long, coiled gut (*A. spilurus*), one predatory piscivore with an elongated body and highly protrusbile jaws (*P. splendida*), two substrate sifters that feed extensively on benthic invertebrates (*A. robertsoni* and *T. meeki*), one midwater invertebrate feeder (*C. salvini*), and one large-bodied, trophic generalist (*V. maculicauda*). In this cichlid assemblage, each species seems to possess

ecological requirements that are supported by morphological and behavioral adaptations that enable them to partition diet and habitat resources within the community.

The present study provides not only basic ecological data essential for effective conservation, but also evidence of niche diversification within a local assemblage of heroine cichlids that will be useful for ecological and evolutionary analyses at larger scales of taxonomy, geography, and time. While studies of adaptive radiation among African cichlids have extensively shown that adaptive radiation related to trophic morphology and behavior has led to coexistence of many closely related species, there have been few quantitative studies of adaptive radiation in the Neotropics (Fryer and Iles 1972, Greenword 1974). This information will contribute to a growing body of ecological data from Neotropical cichlid assemblages that, when analyzed in conjunction with phylogenetic data, will determine whether or not ecological and morphological patterns within the Heroini reflect an adaptive radiation.

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